

R.M. McDowall

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New Zealand Freshwater Fishes

an Historical and Ecological
Biogeography



New Zealand Freshwater Fishes

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New Zealand Freshwater Fishes

An Historical and Ecological Biogeography

 Springer

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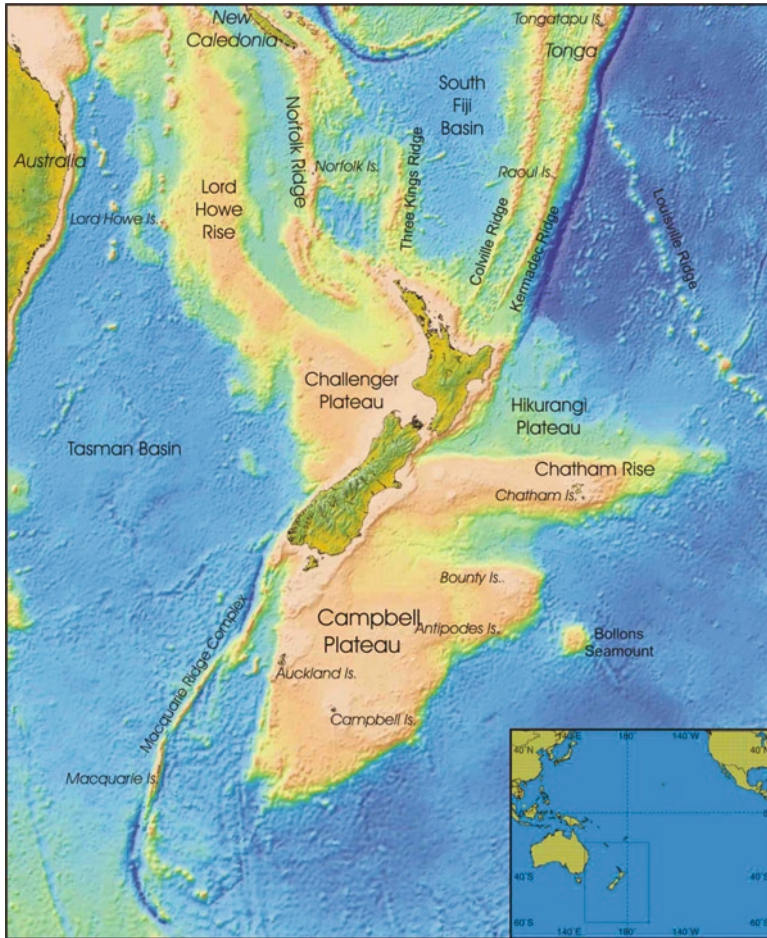
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Zealandia, a substantial ancient continent that is now evident as a series of emergent islands, of which New Caledonia and New Zealand are much the largest, these and other small islands being connected by various submerged rises and plateaus (GNZ Science, Wellington, N Z)

Preface

In many ways, this book is the culmination of more than four decades of my exploration of the taxonomy, biogeography and ecology of New Zealand's quite small freshwater fish fauna. I began this firstly as a fisheries ecologist with the New Zealand Marine Department (then responsible for the nation's fisheries research and management), and then with my PhD at the Museum of Comparative Zoology at Harvard University, Cambridge, MA, USA in the early–mid 1960s. Since then, employed by a series of agencies that have successively been assigned a role in fisheries research in New Zealand, I have been able to explore very widely the natural history of that fauna. Studies of the fishes of other warm to cold temperate southern lands have followed, particularly southern Australia, New Caledonia, Patagonian South America, the Falkland Islands, and South Africa and, in many ways, have provided the rather broader context within which the New Zealand fauna is embedded in terms of geography, phylogeny, and evolutionary history, and knowing this context makes the patterns within New Zealand all the clearer.

An additional stream in these studies, in substantial measure driven by the behavioural ecology of these fishes round the Southern Hemisphere, has been exploration of the role of diadromy (regular migrations between marine and freshwater biomes) in fisheries ecology and biogeography, and eventually of diadromous fishes worldwide. In part this interest was stimulated by my discovery in the 1960s of the role of diadromy in the New Zealand fauna. This work was enhanced by discussions of the phenomenon with American George Myers, who introduced the term diadromy to the lexicon of ichthyology, and then an invitation to present the keynote paper at a meeting of the American Fisheries Society in Boston, in 1986. This plunged me into the study of diadromy across a broad range of geographical and taxonomic perspectives, has resulted in numerous papers, and has formed the basis for several books, including the present one. In the 25 years since that conference, others have focussed on the place of diadromy in the global historical ecology of diadromous fishes, including several in Hawaii, where all the freshwater fishes are diadromous gobioids, and others in Bordeaux, France in 2005 and a repeat of the American Fisheries Society symposium held in Halifax, Nova Scotia, in 2007.

As I came to understand the New Zealand fauna better, and began to perceive the much greater diversity of freshwater fish faunas in other lands, especially North and South America, Africa, and Asia, it became obvious to me that the modest

New Zealand fauna (<40 species) was large enough to have the basic material within which to explore biogeographical patterns and processes, and provided the opportunity to master knowledge and explore pattern and process, cause and effect, evolution and biogeography, in a way that would have been much more difficult in areas with more speciose faunas – one individual can come to know intimately the distribution and ecology of a small fauna as New Zealand's in a way that permits one to ask and endeavour to answer questions that would be much more difficult in a larger fauna. As an essential background to these studies has been the richly explored knowledge of New Zealand's historical geology, within which the freshwater fish fauna has evolved and diversified. Additional to these streams of knowledge has been the emergence of DNA sequencing technology. This has firstly provided a much clearer perspective on the taxonomic diversity of the fauna, and has provided knowledge of distribution patterns of genetic lineages that no self-respecting ichthyologist could have predicted from patterns of taxonomic diversity and its distribution. So, all these streams of interest, knowledge and activity have converged for me over the past 45 years, provided the opportunity to explore the fauna in a distinctive way that results in this small book. Biogeography is an exceptionally fertile field for New Zealand biologists, as many international authors have recognised. This is a result of the country's former place as a fragment of Gondwana, its early separation from Gondwana, and its long geographical isolation in the southwestern Pacific Ocean and, perhaps, also its relatively large size, at least among the islands of the globe. Historical geology is a very active science in New Zealand, providing the essential knowledge in which biogeography is embedded. Strong debate persists, particularly relating to whether there was emergent land in the New Zealand landmass throughout the Cenozoic. There are strong schools of thought that suggest, on the one hand, that at some stage during the Cenozoic all of New Zealand was submerged by sea, whereas others are arguing that there must have been some emergent land continuously since New Zealand detached from Gondwana. This sort of debate is healthy, and the last word has certainly not been heard on this story. At the same time, biogeography as a subject has been highly controversial, wracked with deep debate and schism as to method. I think that, too, is healthy and is bringing a sharp focus on New Zealand as a microcosm of global biogeography. It has been stimulating fun (mostly!) being involved in these debates and controversies.

I am indebted to the New Zealand Government and its various research agencies that have allowed me the freedom to explore natural history very widely and with few limits or constraints. For too many years I was 'lost in the wilderness of bureaucracy', being a middle-level science administrator, a role that I brought to an end in 1991 by asking to be demoted, and I returned to the work bench and microscope, perhaps the best choice, at least for me. Since then, my last employer, the National Institute of Water and Atmospheric Research, has perpetuated that freedom (at least as far as the strictures of the modern science administrative environment allows). Then, the award of a James Cook Research Fellowship by the Royal Society of New Zealand, from 1999 to 2001 made this freedom even greater, and the prospect of returning to a full time research career in the modern environment had little

appeal and I effectively retired, and I have continued to work with logistic and facility support of NIWA in the years since holding the fellowship. Many colleagues have contributed with both specimens and ideas over many years. In particular, Greg Kelly has contributed with his meticulous drafting of many of the figures, and with his patience, as these have evolved and have needed to be redone or amended to meet my exacting needs.

Christchurch, New Zealand
November 2009

R.M. McDowall

Volume Foreword

There is a well-established tradition of ichthyological books in the form of “The Fishes of (your favorite region)”. It is a peculiar feature of those books that they often deal with a political, rather than biogeographical region. Bob McDowall’s unique achievement is a remarkable work on both a political and biogeographical region. This will be the definitive book of its kind and a model for all who attempt a book of fishes of their region. Of course that is because New Zealand is such a remarkable place – as McDowall makes clear to us. New Zealand is responsible not only for the nature of this definitive book but also for the remarkable nature of Bob McDowall himself.

There is no more definitive work possible on the freshwater fishes of New Zealand, because there is no better - informed or more clearly opinionated author than Bob McDowall. It is entirely appropriate that he should complete this statement of his life’s work in 2009, the sesquicentennial of the publication of “On the Origin of Species” (Darwin 1859). McDowall quotes extensively from Darwin’s various writings in reaching his own conclusions about New Zealand’s freshwater fishes. He also draws upon an encyclopedic wealth of knowledge from subjects as diverse as paleontology, geology, human history and molecular genetics to support his ichthyological conclusions. It is no exaggeration to compare McDowall’s interpretation of New Zealand favorably to Darwin’s interpretation of oceanic islands (Darwin 1839). Both depend considerably on an understanding of geology and volcanism as creative forces in biological evolution on remote oceanic islands. Both consider the broader aspects of the remarkable flora and fauna on those islands.

We have long known something about the freshwater fishes of New Zealand – largely as a result of the publications by Bob McDowall. Now we understand a great deal about the freshwater fishes – and New Zealand itself – as a result of this publication by him. Now we truly appreciate his “Mona Lisas” of New Zealand’s natural world. In doing so he has focused our attention on the process, as well as the pattern. As we would expect, the origins and life histories of the freshwater fishes of New Zealand occupy a major part of this publication, and are the basis for a broader understanding of fish migrations and distribution. This book is really a major contribution to biogeography, cleverly disguised as a tome on the freshwater fishes of New Zealand. A more appropriate title might be, “On the Origin of New Zealand Freshwater Fish Species”.

References

- Darwin, C. R. 1839. Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe. Journal and remarks. 1832-1836. London: Henry Colburn.
- Darwin C. R. 1859. On the Origin of Species by means of natural selection or the preservation of favoured races in the struggle for life. James Murray, London.

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Chapter 1

New Zealand's Distinctive and Well-Known Freshwater Fish Fauna

Abstract New Zealand is a small archipelago at temperate latitudes in the southwestern Pacific Ocean, and has been isolated there since separating from Gondwana about 80 million years ago. Its freshwater fish fauna was discovered beginning with visits by James Cook in the late eighteenth century, and Charles Darwin in the 1830s. Early descriptions of the fauna were by European ichthyologists, but locally domiciled workers took over in the last third of the nineteenth century and the fauna's taxonomy was substantially clarified by amateur naturalist Gerald Stokell in the 1940s and 1950s. In the modern era the advent of DNA sequencing technology has led to clarification of the taxonomy and the recognition of new cryptic taxa. Additional species have appeared in the fauna towards the end of the twentieth century through natural dispersal and possibly discharges of ships' ballast water. Today, c. 40 species are recognised, over half in the family Galaxiidae, with the second largest group being Eleotridae. A modest diversity of fossil taxa has been found, mostly from Miocene lake deposits, including at least one belonging to a perciform family not otherwise known from New Zealand.

Keywords DNA sequencing • Eleotridae • Fossils • Galaxiidae • History • New Zealand • Perciforms • Taxonomy

1.1 Introduction

New Zealand is a slender archipelago of islands, highly isolated geographically in the warm to cool temperate southwestern Pacific Ocean (Fig. 1.1). This isolation, which has been long-lasting from late Mesozoic times, has had profound biogeographical implications, as much for the region's freshwater fish fauna as for other components of the biota, and exploring these implications is the subject and purpose of this book.

The New Zealand freshwater fauna is of quite modest size with, at the time of writing, just 38 formally described species, as well as several presently undescribed lineages. These are listed in Table 1.1, where the family affiliations, scientific and

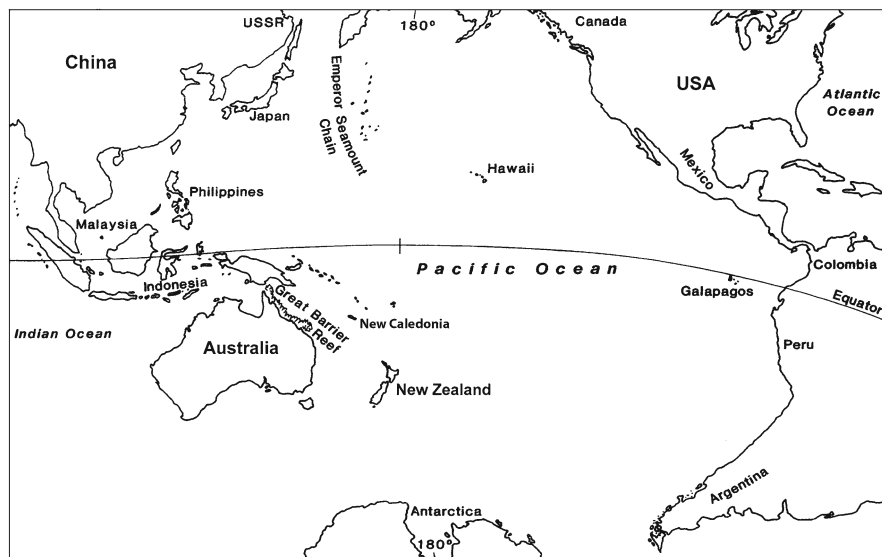


Fig. 1.1 New Zealand and its broader setting in the southwestern Pacific Ocean

common names are also given (common names are used widely, hereafter). Until relatively recently, only 27 species were recognised (McDowall 1990), but much has changed in recent decades, and the latest studies, especially with the emergence of gene sequencing technology (Avice 2009), are providing a radically different perspective on the fauna. In fact it is that technology that has provided much improved understanding of both the taxonomic diversity of the fauna as well as of its phylogenetic relationships, knowledge of these relationships that is, in turn, greatly clarifying our understanding of the fauna's history and biogeography.

The fauna compares quite closely in size with that in Great Britain, where about 40 species are recognised (Maitland and Campbell 1992), or is rather smaller than the 95 species recognised from Japan (Matsuura et al. 2000), both these island nations of rather similar geographical area to New Zealand and at similar northern latitudes to New Zealand in the south, though both Great Britain and Japan were connected to continental masses relatively recently, and this of course has significant implications for the spread of freshwater fishes (a distinct contrast with New Zealand's very long geographical isolation, for perhaps 80 million years). And though New Zealand's fauna is quite small, it is nevertheless big enough to display significant ecological, evolutionary and taxonomic diversity, and so to create interest among naturalists, especially ichthyologists and biogeographers.

There are lots of distinctive aspects, especially when one recognises that, in addition to New Zealand's great and long-lasting geographical isolation in the warm to cold-temperate southwestern Pacific Ocean, it has also had a highly complex and varied geological and climatic history (see Chapter 2); there is a widespread view that freshwater fishes are of special biogeographical interest owing to the perception

Table 1.1 List of freshwater fish species

Species (by family)	Common name	Endemic (End); Indigenous (Indig)	Species diadromous	Indigenous species with landlocked populations	Chief habitat types (most favoured is <u>underlined</u>)
Family Geotriidae					
<i>Geotria australis</i>	Lamprey	Indig	Y	Never	Stream
Family Anguillidae					
<i>Anguilla australis</i>	Shortfin eel	Indig	Y	Never	Stream/wetland, at low elevations
<i>Anguilla dieffenbachii</i>	Longfin eel	End	Y	Never	<u>Stream/lake</u>
<i>Anguilla reinhardtii</i>	Spotted eel	Indig	Y	Never	<u>Stream</u>
Family Retropinnidae					
<i>Retropinna retropinna</i>	Common smelt	End	Y	Often	<u>Stream/lake</u>
<i>Stokella anisodon</i>	Stokell's smelt	End	Y	Never	<u>Stream</u>
<i>Prototroctes oxyrhynchus</i>	Grayling	End	Y	Never	<u>Stream</u>
Family Galaxiidae					
<i>Galaxias anomalus</i>	Otago roundhead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias argenteus</i>	Giant kokopu	End	Y	Occasional	<u>Stream/lake</u>
<i>Galaxias brevipinnis</i>	Koaro	Indig	Y	Often	<u>Stream/lake</u>
<i>Galaxias cobitis</i>	Lowland longjaw	End	N	N/A	<u>Stream</u>
<i>Galaxias depressiceps</i>	Taieri flathead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias divergens</i>	Dwarf galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias eldoni</i>	Eldon's galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias fasciatus</i>	Banded kokopu	End	Y	Occasional	<u>Stream/lake</u>
<i>Galaxias gollumoides</i>	Gollum galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias gracilis</i>	Dune lakes galaxias	End	N	N/A	<u>Lake</u>
<i>Galaxias macronasus</i>	Roundnose galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias maculatus</i>	Inanga	Indig	Y	Rarely	<u>Stream/lake</u>

(continued)

Table 1.1 (continued)

Species (by family)	Common name	Endemic (End); Indigenous (Indig)	Species diadromous	Indigenous species with landlocked populations	Chief habitat types (most favoured is <u>underlined</u>)
<i>Galaxias paucispindylus</i>	Alpine galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias postvectis</i>	Shortjaw kokopu	End	Y	Never	<u>Stream</u>
<i>Galaxias prognathus</i>	Upland longjaw galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias pullus</i>	Dusky galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias</i> 'species D'	Clutha flathead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias</i> 'southern'	Southern flathead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias</i> 'northern'	Northern flathead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias</i> 'Teviot'	Teviot flathead galaxias	End	N	N/A	<u>Stream</u>
<i>Galaxias vulgaris</i>	Canterbury galaxias	End	N	N/A	<u>Stream</u>
<i>Neochanna apoda</i>	Brown mudfish	End	N	N/A	<u>Wetland</u>
<i>Neochanna burrowsius</i>	Canterbury mudfish	End	N	N/A	<u>Wetland</u>
<i>Neochanna diversus</i>	Black mudfish	End	N	N/A	<u>Wetland</u>
<i>Neochanna heletos</i>	Burgundy mudfish	End	N	N/A	<u>Wetland</u>
<i>Neochanna rekohua</i>	Chathams mudfish	End	N	N/A	<u>Lake</u>
Family Pinguipedidae					
<i>Cheimarrichthys fosteri</i>	Torrentfish	End	Y	Never	<u>Stream</u>
Eleotridae					
<i>Gobiomorphus alpinus</i>	Tandale bully	End	N	N/A	<u>Lake</u>
<i>Gobiomorphus basalis</i>	Cran's bully	End	N	N/A	<u>Stream</u>
<i>Gobiomorphus breviceps</i>	Upland bully	End	N	N/A	<u>Stream/lake</u>
<i>Gobiomorphus cotidianus</i>	Common bully	End	Y	Often	<u>Stream/lake</u>
<i>Gobiomorphus hubbsi</i>	Bluegill bully	End	Y	Never	<u>Stream</u>
<i>Gobiomorphus huttoni</i>	Redfin bully	End	Y	Never	<u>Stream</u>
<i>Gobiomorphus gobioides</i>	Giant bully	End	Y	Never	<u>Stream</u>
Family Pleuronectidae					
<i>Rhombosolea retitarta</i>	Black flounder	End	Y	Never	Estuaries and lowland rivers and lakes

of their particular difficulty in spreading geographically, owing to the isolated and fragmented nature of freshwater ecosystems, as Darwin (1859), long ago recognised, and this is particularly pertinent to understanding the diversity and distribution patterns of freshwater fish faunas. New Zealand is of much interest, too, in the sense that the biogeographical patterns and processes associated with its New Zealand fauna and flora can perhaps be viewed as a global microcosm (McDowall 2008), representing at a small scale what has happened much more widely.

The New Zealand freshwater fish fauna is very well known in terms of its taxonomy, life histories and geographical distributions (McDowall 1990, 2000a). This combination of attributes makes the fauna of particular interest from a biogeographical perspective. Notable is a complete absence of what Myers (1938, 1949, 1951) and Darlington (1957) referred to as ‘primary’ freshwater fishes – groups that are regarded as having very low tolerances of marine water salinities. It seems certain that primary freshwater Ostariophysan fishes of the orders Cypriniformes (carps), Characiformes (characins) and Siluriformes (catfishes) were once present on Gondwana, as these groups are variously widely present on Africa and South America, but whether or not any members of these groups were ever present on New Zealand, which was also once a part of Gondwana (see Chapter 2), there are certainly none there now, and there is no hint of any of them having ever been present in New Zealand. There are a few catfishes in Australian, but these are regarded as salinity tolerant or derived from groups that are. And there are some other Australian freshwater fish taxa that may be ancient, Gondwanan primary freshwater fish groups: the Ceratodontidae (lungfishes), Osteoglossidae (saratogas), and perhaps even the relictual *Lepidogalaxias* (salamanderfish – Fig. 1.2), but none of these is known from New Zealand. Whether this absence of primary freshwater fish groups from New Zealand reflects the fact that they have never been present, or rather that they were once present but were extinguished by the very robust and complex geological and climatic histories of New Zealand, is unknown, and is likely to remain so unless relevant fossils eventually reveal such presence. Certainly, there is no known hint of their presence, but absence is much more difficult to prove conclusively than presence.

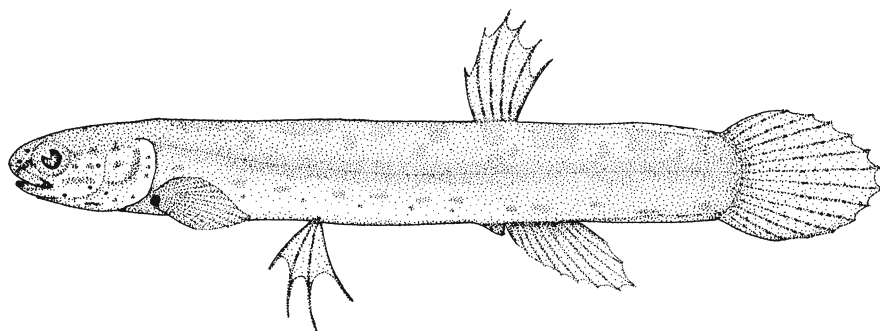


Fig. 1.2 The Western Australian salamanderfish, *Lepidogalaxias salamandroides*, 71 mm TL (family Lepidogalaxiidae): a relictual species of distinctive specialisation and uncertain relationships

1.2 The Extant Fauna Known to Polynesian Maori

Freshwater fishes were well known to New Zealand's indigenous Polynesian Maori people prior to European settlement, as many species were of great importance to them as sources of protein (McDowall in press). Species of dietary significance to Maori included a lamprey (*Geotria australis*) and freshwater eels (*Anguilla* spp.), the latter being present in huge abundance and some of them among the largest freshwater eels known. But other groups of more distinctive, local, character were also important to Maori, such as:

- A so-called 'southern grayling' (*Prototroctes oxyrhynchus*: Fig. 1.3), though it was nothing like the Northern Hemisphere grayling, *Thymallus* (family Salmonidae).
- The southern smelts' (*Retropinna retropinna*, *Stokellia anisodon*), which would seem highly familiar to biologists from high northern latitudes as they resemble the osmerid smelts (f. Osmeridae) from boreal North America and Europe and the two families are closely related (McDowall 1969; Johnson and Patterson 1996).
- Much more distinctive and unfamiliar are various sorts of 'native trout' that were known to Maori as 'kokopu' and 'inanga' (*Galaxias* spp., family Galaxiidae: Fig. 1.4); these look nothing like Northern Hemisphere trouts of the family Salmonidae, nor any other group of fishes, for that matter; and there are so-called 'mudfishes' (genus *Neochanna*, Fig. 1.5, also in the family Galaxiidae).
- There is also a variety of smaller fishes such as a torrentfish (*Cheimarrichthys fosteri*: family Pinguipedidae: see Fig. 7.5) that look little like anything else.
- Several small fishes known locally as 'bullies' (*Gobiomorphus* spp.: family Eleotridae: Figs. 1.6, 1.7), and which resemble the more familiar 'gobies' of the family Gobiidae.
- And there is a freshwater flounder (genus *Rhombosolea*, family Pleuronectidae), that looks just like any flounder.

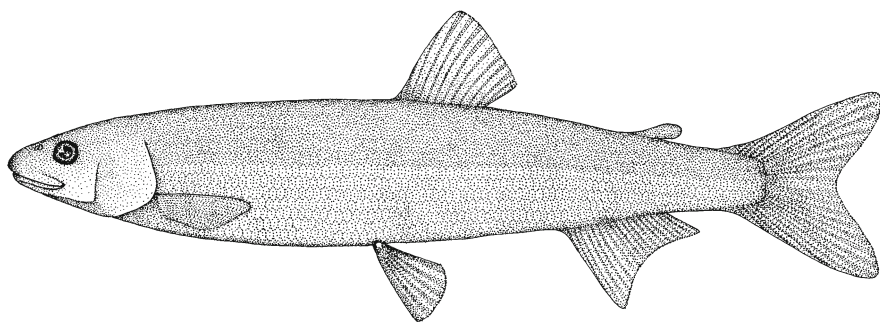


Fig. 1.3 The New Zealand grayling, *Prototroctes oxyrhynchus* (family Retropinnidae), 220 mm LCF

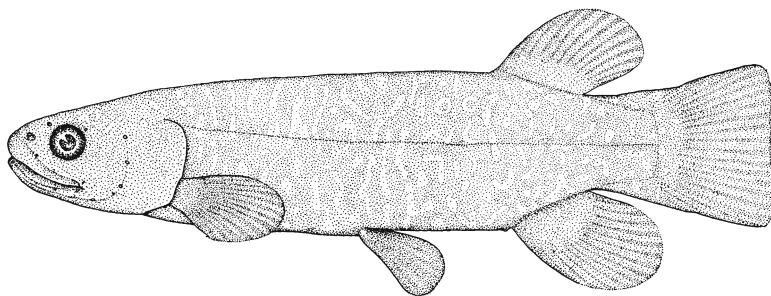


Fig. 1.4 The giant kokopu, *Galaxias argenteus* (family Galaxiidae), 240 mm LCF, the largest known galaxiid, first collected by the Forsters from Dusky Sound, Fiordland, in the remote southwestern South Island of New Zealand

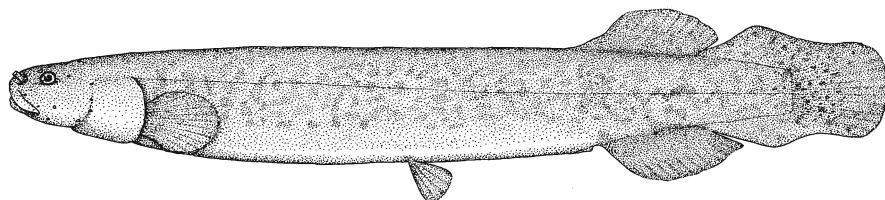


Fig. 1.5 Canterbury mudfish, *Neochanna burrowsius*, 124 mm TL (family Galaxiidae)

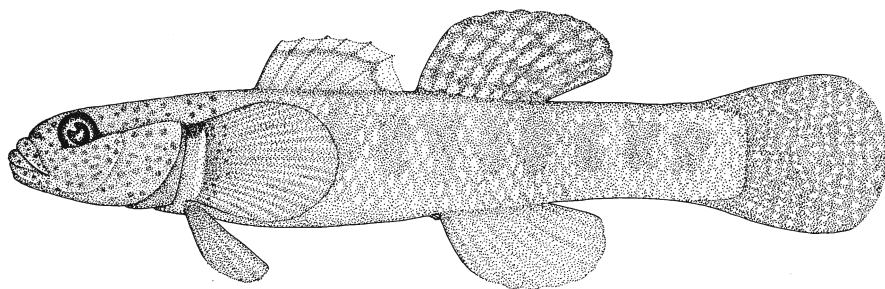


Fig. 1.6 Male bluegill bully, *Gobiomorphus hubbsi*, 65 mm TL (family Eleotridae)

1.3 Scientific Discovery and Formal Description of the Fauna: the Place of European Biologists

Scientific recognition and description of this freshwater fish fauna began almost with the earliest visiting European seafarers and explorers to reach New Zealand. Dutchman Abel Tasman was the first to find his way to New Zealand, in 1742 (King 2007), but he made no natural history observations. Joseph Banks, the naturalist with James Cook on his initial voyage to New Zealand in 1769 seems not to have

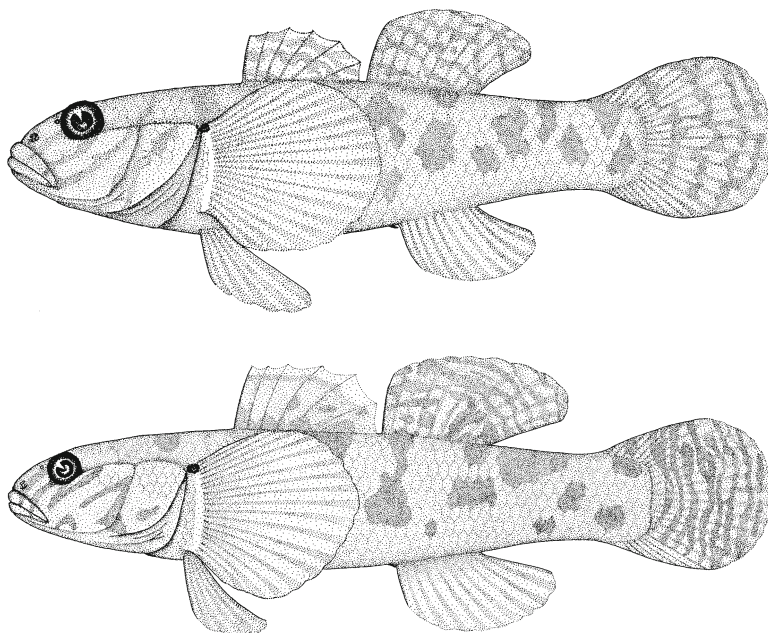


Fig. 1.7 Pair of redfin bullies, *Gobiomorphus huttoni*: A. female, 78 mm TL; B. male, 105 mm TL (family Eleotridae), showing difference in fin sizes

collected any freshwater fishes, though he observed diverse other sorts of natural life, including marine fishes. John Reinhold Forster and his son George were the naturalists on board the *Resolution* when James Cook came back to New Zealand in 1773, and they caught what is now known as giant kokopu (*Galaxias argenteus* – Fig. 1.4) from Lake Forster, which drains via Cook Stream into Pickersgill Harbour (all of these places being named for individuals on Cook's second expedition), in Fiordland on the mountainous west coast of the southern South Island of New Zealand. This is where Cook and his crew spent several weeks making astronomical observations and they also undertook ship maintenance there (Begg and Begg 1969). Much later, inanga (*Galaxias maculatus*) were collected by Charles Darwin from streams in the Bay of Islands in the northeastern North Island of New Zealand in 1835, and these were taken back to Britain for description (Jenyns 1842). And the subsequent early records of the capture of freshwater fishes from New Zealand are a litany of other notable nineteenth century European explorers, seafarers and naturalists of varied other nationalities who visited New Zealand (including Italians, French, Germans, Austrians, Russians, Americans, and others).

Some of the early described freshwater fish species had distinctly tortuous nomenclatural histories, as for instance:

- The several descriptions of the specimen collected by the Forsters, mentioned above. Amongst other descriptions of this same specimen was one by the Germans Bloch and Schneider (*Galaxias alepidotus* in 1801), ostensibly based

on the same fish that the Forsters had collected; this species later redescribed as *Gl. grandis* by von Haast (1873) and *Gl. kokopu* by Clarke (1899). (Because the generic names *Galaxias*, and *Gobiomorphus* are used so often through this book, where the generic names are abbreviated I have adopted the convention of abbreviating these to *Gl.* and *Gb.* respectively).

- The Frenchmen Cuvier and Valenciennes (1837) described the eleotrid *Gobiomorphus gobioides* (as a species of *Eleotris* in 1837, known today as ‘giant bully’). Its description was based on specimens collected in New Zealand by the Frenchmen Quoy and Gaimard, who were in New Zealand on the *Astrolabe* in 1827 (McDowall 1964a). As it happens, the two specimens that Quoy and Gaimard collected, and which formed the basis for Cuvier and Valenciennes’ description, actually represented two distinct species, one being what is still known as *Gb. gobioides*, the other a different fish now known as *Gb. huttoni* (McDowall 1964a, 1971).

Not surprisingly, however, given New Zealand’s largely British colonisation and its early annexation by the British in 1840 (King 2007), it was British naturalists who were soon most prominent in studying the fauna, especially ichthyologists working at the British Museum in London. Names such as John Gray (1842 – longfin eel, *Anguilla dieffenbachii*, and Cran’s bully, *Gobiomorphus basalis*), Richardson (1848 – shortfin eel, *Anguilla australis* and New Zealand smelt, *Retropinna retropinna*) and Albert Günther (1867 – brown mudfish, *Neochanna apoda*, and 1870 – grayling, *Prototroctes oxyrhynchus*) feature as the authors of early species’ names applied to our fauna (see McDowall 1970, 1990, 2000a). Here we see a group of biologists of wide international reputation in the mid-nineteenth century.

1.4 Local New Zealand Naturalists Take Over

Before long, as New Zealand became settled by colonials from Europe, again mostly from Great Britain, local naturalists developed an interest in native fishes, and also the confidence to describe them, so that there was a shift from largely British domiciled workers to almost entirely local biologists discovering and describing the fauna during the 1870s. This move was led by chief luminaries of colonial natural science in New Zealand of the time, such as James Hector, Frederick Hutton, and Julius von Haast, and their names are associated with seven still used species’ names, the others being reduced to synonyms. These species described included:

- The so-called New Zealand grayling, redescribed in 1871, in ignorance of the earlier Günther description, by Hector as *Retropinna upokororo* and thus a junior synonym of *Prototroctes oxyrhynchus* – Fig. 1.3).
- A freshwater flounder, *Rhombosolea retiaria*, described in 1873 by Hutton.
- The so-called torrentfish, *Cheimarrichthys fosteri*, described in 1874 by von Haast.

All of these men were, of course, colonists who had done any scientific training overseas, and had come to New Zealand as adults. Thus, by about the early-mid

1870s, most of the overseas contribution was over and the description of new species was, thereafter, largely by New Zealand domiciled workers. Notable was description of several species of *Galaxias* by colonial surveyor Francis Clarke (1899) including:

- *Galaxias kokopu* (a junior synonym of *Gl. argenteus* – as noted earlier).
- *Galaxias robinsonii* (a junior synonym of *Gl. brevipinnis*).
- *Galaxias postvectis*, the only Clarke name to survive, though it lay lost in the literature for 60 years until it was ‘rediscovered’ and restored to use by amateur naturalist Gerald Stokell in 1960.

There were some exceptions to local description during the last two decades of the nineteenth century, and later, including:

- The 1880 description of a species of *Galaxias* from Campbell Island by Frenchman H.E. Sauvage (*Gl. campbelli* – a junior synonym of another previously described species, *Gl. brevipinnis* – McDowall 1970).
- Description of the redfin bully, *Gb. huttoni*, by Australian James Ogilby (1894), a valid name still in use (McDowall 1964a).
- Description of *Gl. huttoni* from New Zealand by British ichthyologist C. Tate Regan (1905), which is yet another junior synonym of *Gl. brevipinnis* (McDowall 1970).
- Publication of an unnecessary replacement name (*Gb. stokelli* for *Gb. huttoni*) by Australian Gilbert Whitley (1956).
- In addition a couple of species were described by a New Zealander in tandem with the same Australian (*Gl. charlottae* and *Gl. castlae*, described by Whitley and Phillipps 1939 – both again proving to be junior synonyms of already named and described species, *Gl. postvectis* and *Gl. brevipinnis* respectively – McDowall 1970).

Thus the ‘success’ rate of these somewhat later overseas contributors to the now accepted taxonomy of the fauna, and to knowledge of New Zealand’s freshwater fish biodiversity, was quite poor – only one name survives as valid. In part this lack of success was due to the authors tending to use typological approaches to taxonomy (Mayr 1942), and to their having only fragmentary knowledge of the fauna, and often because usually they had very few specimens to work with. This listing does, however, indicate the extent to which early biologists, both international and local, struggled to establish some order and stability in the fauna’s taxonomy.

There was further taxonomic activity in the 1920s when then New Zealand’s Dominion Museum employee, William Phillipps, became involved with the study of native freshwater fishes (as well as with birds and a variety of ethnographic subjects). In addition to the work he published in association with Australian Gilbert Whitley, mentioned above, Phillipps described several new species, in particular:

- The Canterbury mudfish, now known as *Neochanna burrowsius* (family Galaxiidae – Fig. 1.5) (Phillipps 1926).

- *Gl. koaro* (Phillipps 1940), now regarded as yet another synonym of *Gl. brevipinnis* (McDowall 1970).
- Phillipps (1925) also inappropriately gave new names to both New Zealand's freshwater eels – *Anguilla schmidtii* for the shortfin eel and *A. waitei* for the longfin eel (both now also synonyms of earlier, well-established names); for many years the name *schmidtii* was used to denote an ostensibly distinct New Zealand subspecies of *A. australis* (the other subspecies was Australian), but the sub-specific distinction is not regarded as useful and it has, on the whole, been discarded for that reason (McDowall 1990; Dijkstra and Jellyman 1999).

Phillipps also published a series of brief, species-by-species synopses of knowledge of diverse freshwater fishes that are useful in a limited way and do record some early knowledge of the species among New Zealand's Polynesian Maori people (Phillipps 1919, 1923a, b, 1924a, b, 1925, 1926, 1929).

1.5 Clarifying a Century of Taxonomic Confusion

It would not be until the work of angler and amateur naturalist Gerald Stokell, from the 1930s to 1960s that the detail of the fauna would begin to crystallize in an enduring way. Stokell's interest developed initially through involvement with the Council of the North Canterbury Acclimatisation Society that was involved in the local management of trout fisheries based on introduced salmonid species (McDowall 1975a, 1994a). Stokell began with a series of studies of trout feeding, condition and parasites in Lake Ellesmere, a large, shallow, brackish/tidal lake, near his home south of Christchurch (Stokell 1928, 1936, 1938a). However it was not long before the native freshwater fish began to capture Stokell's interest largely, it seems, because he found himself unable to give names to many of the fish he was encountering, and their study became a consuming passion for the rest of his life. To Stokell credit should be given for establishing considerable order out of the reigning chaos in freshwater fish taxonomy (McDowall 1975a). In a series of sometimes substantial papers, beginning in 1938 and lasting for about 30 years, Stokell published family by family revisions of the fauna, interspersed with smaller papers correcting perceived errors in nomenclature and/or describing the new species as he discovered them (Stokell 1938b, 1939, 1941a, b, 1945, 1949a, b, 1954, 1959, 1960, 1962, 1966).

Stokell's technical knowledge of ichthyology was, not surprisingly, quite limited (he seems to have made a living growing orchids – McDowall 2000b). Moreover, he did not have a good understanding of the complex protocols of the International Code of Zoological Nomenclature (ICNZ), which was important for making correct taxonomic decisions. Stokell, as well, not having a good grasp of the nature and taxonomic significance of phenotypic variation in fishes, adopted an approach to taxonomy that was strictly typological. As a result he made mistakes, though few if any of them have proved to have had long term and serious repercussions.

Perhaps the most obvious of these mistakes was his choice of the Jenyns' (1842) name *Gl. maculatus* to have nomenclatural priority over *Gl. attenuatus*. Both names were used for fish collected by Darwin on the *Beagle* voyage, in Chile and New Zealand (Jenyns 1842). Stokell made his decision on the stated, but erroneous, grounds that the former name had "page priority" over the latter (i.e. it appeared on an earlier page in Jenyns 1842). The ICNZ recognises no such thing as page priority, but as both names were published by Jenyns (1842), each has equal nomenclatural priority, and choosing which name is to be used falls to the first reviser. Thus all that Stokell had done was to make a decision on priority, which was his right as first reviser, but he had nominated an erroneous reason for making his choice. This did not invalidate his decision.

Interestingly, when noted American ichthyologist Carl Hubbs visited New Zealand for the 7th Pacific Science Congress in 1949, he went fish collecting with Stokell, and the pair discovered the bluegill bully, a species of *Gobiomorphus* (family Eleotridae). Stokell's hope was that Hubbs would describe this fish, which had hitherto escaped recognition (Stokell 1955). Evidently Stokell found Hubbs tardy at doing so, finally lost patience, and described the fish himself, giving it the specific name *hubbsi* (Stokell 1959 – Fig. 1.6) – a likely satisfactory outcome for Hubbs. It seems, today, extraordinary that this very widespread, locally abundant, and very distinctive species was not first recognised until so late in New Zealand history, though its very swift, torrent-water habitat probably meant that it had never before been collected. If Stokell had seen it before Hubbs' visit, he would surely have recognised it and described it, so it was clearly new to him. It is interesting to imagine the pair at work collecting fishes in New Zealand rivers, one (Hubbs) being immensely experienced with fishes from many parts of the world, but having little or no local knowledge, but the other (Stokell) having rather rudimentary knowledge of ichthyology as a science but experienced in conditions in New Zealand rivers and the fish that lived there. Hubbs would have seen the newly discovered fish intriguing in terms of where it was collected from (very swift rapids), and its adaptations to that habitat, whereas Stokell would immediately have known that it was totally new to science and hitherto undescribed.

While history has not been greatly generous to Stokell in the number of his species names that remain in use as senior synonyms, he nevertheless is the author of more valid names than anyone else, and may well remain so. Stokell assigned names to 15 new species, of which 10 remain in use as senior synonyms. And it is only fair to note that two Stokell species that were formerly treated as junior synonyms of other names (*Gl. anomalus* Stokell 1959 as a synonym of *Gl. vulgaris* Stokell 1949b, by McDowall 1970, and *Gobiomorphus alpinus* Stokell 1962 as a junior synonym of *Gb. basalis* Gray 1842, by McDowall 1975b) have subsequently been restored to use as senior synonyms (McDowall 1994b; McDowall and Wallis 1996; McDowall and Stevens 2007), vindicating Stokell's original descriptions of the fish as distinct taxa.

Of as much significance as his discoveries of new species, in some ways, was the role that Stokell played in unravelling some very tortuous taxonomic situations associated with the fauna's nomenclature. Difficulties with these were exacerbated

by some seriously inadequate original descriptions, and also the failure of early workers to designate type specimens or the subsequent disappearance of the designated types from museum collections. One example is Stokell's assignment of the name *argenteus* used by Gmelin 1789 to the giant kokopu, previously called *Gl. alepidotus* (Bloch and Schneider 1801), and another is his recognition of Clarke's (1899) *Gl. postvectis* as a valid species (even though until the 1960s rarely seen). The primary reason why five of Stokell's names don't survive, and the same applies to several earlier names proposed by others such as Phillipps (1940), was these authors' lack of understanding of phenotypic variation, and specifically, a failure to recognise that widespread diadromous species (those with regular marine life stages – McDowall 1988, 1990, and see Chapter 5) often establish landlocked populations, and that when they do, seemingly fundamental morphological characters, like vertebral number, can undergo major variation (McDowall 2003a). Also, Stokell never apparently realised that the *Gobiomorphus* bullies exhibit strong sexual dimorphism (Fig. 1.7), with the males being larger, stockier, and more brightly coloured than the females (McDowall 1964a, 1990), and this caused him some confusion, e.g., Stokell referred to redfin bullies sometimes having red colouration in the fins, whereas other specimens did not, though he seems never to have realised that this was a sexual distinction, and that it is the males that have the brighter colouration. Otherwise, Stokell made only a couple of fundamental nomenclatural/taxonomic errors. One was to mis-associate the fish that we now know as *Gb. huttoni* (redfin bully) with the name '*radiata*' (which properly is applied to a small marine eleotrid – *Grahamichthys radiatus* Valenciennes – see McDowall 1965). And Stokell also failed to distinguish what we now know as Cran's bully, and appears to have thought that it was a form of, or no different from, the common bully. As a result he erroneously associated the name '*basalis*' of Gray (1842) with the common bully, which remained formally unnamed until 1975 (*Gb. cotidianus* McDowall 1975b).

1.6 The Modern Era

One of the key time/transition points in the history of New Zealand freshwater fish nomenclature is the early 1960s. This was about the time that Stokell's effective contribution ended (no species he described later survives in accepted nomenclature), and it was then that what might be called the "modern era" began. A "biological species concept" (Mayr 1942) supplanted the typological species approach used by Stokell (I doubt that he would have known what 'typological' meant), and the nature of geographic variation began to intrude into an understanding of systematics. This began with Cranfield (1962) unravelling issues relating to the recognition and taxonomic allocation of the name *basalis* to various species of *Gobiomorphus*, mentioned above (though he never formally published this work), and McDowall (1964a) did much the same for the nomenclature of the redfin bully.

Other things happened that are peripheral to the work of freshwater fish systematics but central to the direction that it took:

- We began to understand species' life histories and, as just noted, this would prove to have a major impact on the understanding of geographical variation in morphology.
- With the advent of modern electric fishing equipment (Burnet 1959), sampling of New Zealand's rivers and streams attained an ease that Stokell would never have even dreamed of (and it is a tribute to his tenacity and energy that he found as many of the fish species as he did without such assistance); the use of these machines rapidly resulted in the assembly of much larger and more complete collections of specimens from many more geographical locations than hitherto, and this profoundly affected both our knowledge of previously recognised species, and the discovery of new ones.
- As a result of the advent of electric fishing, accompanied by a rapid rise in interest in native freshwater fishes, both among staff and students within the universities and as well as naturalists in government departments, knowledge of species' distributions grew apace, and the availability of larger samples from across the geographical ranges of the species threw much needed clarity onto what was formerly confusion generated by the availability to Stokell (and also Phillipps before him) of only occasional fish of diverse sizes from widely separated localities.

Growth in knowledge of the natural history of the fauna was also accelerated, and is dealt with elsewhere (McDowall 1990). Relevant here is the renewed interest in taxonomy associated with better collecting equipment, more people working, and better academic training, which provided a new perspective on the fauna. These trends are most easily addressed in the family Galaxiidae partly, of course, because it is much the most speciose family in the fauna (in fact over half the species presently recognised – Table 1.1). By the end of the early colonial era, only six New Zealand galaxiid species were accepted as valid (Regan 1905). The work of Phillipps had added three more by the time he published his small book on the fauna in 1940.

By that time Stokell had already begun his work, and one of the names accepted by Phillipps (1940) was Stokell's (1938b) *Galaxias paucispondylus*, whereas two of the names Phillipps recognised are no longer regarded as valid. Stokell's (1949b) revision of the Galaxiidae included 12 species, four of which he had discovered and described himself. And by 1960, towards the end of the 'Stokell era', there were 16 galaxiids. McDowall's (1970) revision of the family reduced the number to 14, and this involved recognition of two species additional to those of Stokell and Phillipps (but only one, *Gl. gracilis*, is now accepted as distinct – McDowall 1972) and the relegation of four species, accepted or described by Stokell, to synonymy. Taxonomy and nomenclature remained relatively stable through the 1980s and early 1990s, until several series of events, or trends, had a marked impacts on the number of species recognised.

1.6.1 The Exploration of New Geographic Areas

In recent years, several relatively remote geographical areas of New Zealand, that had hitherto been very little unexplored, were sampled. For example, surveys of the remote Chatham Islands, about 800 km east of mainland New Zealand revealed hitherto unknown populations, resulting in a new galaxiid being described (Mitchell 1995; McDowall 2004), and the same has been true of remote, mountainous Fiordland, in the southwestern extremity of the South Island, and of Stewart Island in southern New Zealand (McDowall and Chadderton 1999).

1.6.2 Osteological Studies

Osteological and other morphological investigation showed that Mitchell's (1995) endemic galaxiid, described from the Chatham Islands, had been based on juvenile specimens, and with the collection of adult material it became obvious that this species belongs with the *Neochanna* mudfishes (McDowall 2004), a view confirmed by molecular studies (Waters and McDowall 2005).

1.6.3 The Interaction of Genetics and Ecology

Ecologists and geneticists working together at the Zoology Department of the University of Otago discovered inconsistencies in the taxonomy of inland galaxiids in the upper Taieri River in the southeastern South Island as their genetic studies helped to focus on different morphologies (Allibone et al. 1996), and the outcome was recognition of two distinct species there. One of these proved to be Stokell's (1959) *Gl. anomalus* (that had been synonymised with his *Gl. vulgaris*, by McDowall 1970), and the other was new, and was later described as *Gl. depressiceps* by McDowall and Wallis (1996).

This, in turn led to re-examination of another population of this general morphotype in southern New Zealand, which had earlier been recognised as interesting but not taxonomically distinct from the vicinity of Lake Mahinerangi (also in the Taieri catchment) by McDowall (1970) as well as other 'different' populations from the lower Taieri. These were concluded to be two distinct species and were described as *Gl. pullus* and *Gl. eldoni* (McDowall 1997).

1.6.4 The Place of Genetic Studies

Partly this new perspective on the fauna is an outcome of the application of new technologies to our understanding of species diversity and relationships. Initially,

this was prompted by studies of muscle myogens and allozymes, as indicators of the history/evolution of the fauna (Mitchell and Scott 1979; Barker and Lambert 1988; Allibone and Wallis 1993). However, numerous later, and ongoing, studies of mitochondrial and nuclear DNA sequences have been providing novel insights into the taxonomy and phylogenetic relationships of the fauna (Allibone et al. 1996; King and Wallis 1998; Gleeson et al. 1999; Ling and Gleeson 2001; Esa et al. 2001; Wallis et al. 2001; Waters and Wallis 2001a, b; Waters et al. 2000a, 2001a, b; Smith et al. 2003, 2005; Stevens and Hicks 2009). Some of these studies, as noted above, were associated with ecological studies of the galaxiid fauna of the Taieri River in southeastern New Zealand (McDowall and Allibone 1994; Allibone et al. 1996; Allibone and Townsend 1997a, b, 1998; Allibone and McDowall 1997; Allibone 1999), which have together provided clear evidence that our earlier understanding of species diversity in the fauna (McDowall 1970, 1990) was substantially too narrow. This change of perspective was initially stimulated by the discovery that two different genotypes, of a what later proved to be a *Galaxias* species complex were sympatric in a small tributary of the upper Taieri River in southeastern New Zealand (Allibone et al. 1996; McDowall and Wallis 1996). The molecular studies made it possible to reliably allocate individual fish to lineages, helping to clarify their morphological differences, and to diagnose the distinct species.

Stimulated by these discoveries, ongoing molecular studies, based largely on mitochondrial DNA sequencing, have challenged views that had hitherto treated a series of populations of galaxiids widely distributed in the eastern South Island as a single, highly variable species *Gl. vulgaris*, with broad range (McDowall 1970). The newly emerging data have shown that these populations actually represent a species complex (Allibone et al. 1996); six species are now formally recognised in the *Galaxias vulgaris* species group, while at least four additional lineages awaiting further study and decisions on their taxonomic status (Wallis et al. 2001; Waters and Wallis 2000, 2001a, b; Waters et al. 1999, 2001a, b). Much of this newly recognised diversity was found to be in inland Otago and, in several instances, sympatry of distinct lineages has been discovered (Allibone et al. 1996; Esa et al. 2001; Waters et al. 2001a; Wallis and Waters 2003; Crow et al. 2009). However, the implications of these discoveries have been of rather broader significance. These findings have demanded recognition that some of the observed morphological variability is associated with molecular distinctness and, with that, came the recognition and description of new species. The taxonomy of some of these lineages has so far defied clarification from morphological data (McDowall and Hewitt 2004; McDowall 2006), and it is possible that local adaptation at the population scale (ecophenotypes) may be more important than ancestry in influencing morphology among these often very similar and closely-related, sometimes sympatric lineages. As a result, unresolved taxonomic problems remain. Several, of the additional, genetically distinct lineages are proving to be very difficult to distinguish morphologically, diagnose and identify (McDowall and Hewitt 2004; McDowall 2006).

These various southern galaxiid lineages fall into two distinct morphotypes that have become, referred to informally as 'flatheads' and 'roundheads' (see Chapter 11). Among the 'flatheads' is series of six genetic lineages, only two of them formally

described across the entire eastern South Island from north to south: *Gl. vulgaris* sensu stricto and *Gl. depressiceps*. The four roundhead lineages are all southern, in the rivers of Otago, Southland, and Stewart Island and are all formally described: *Gl. anomalus*, *Gl. gollumoides*, *Gl. eldoni* and *Gl. pullus*. And although two of these species, *Gl. anomalus* (a roundhead) and *Gl. depressiceps* (a flathead), were originally described as occurring widely across Otago and Southland (McDowall and Wallis 1996), much ongoing genetic work, only some of it published (Waters and Wallis 2001a, b; Waters et al. 2001a, b), is showing that the scenario is much more complicated and that further lineages may await description as distinct species. The formal outcome of these discoveries remains to emerge, but at the moment various of these lineages remain undescribed and the taxonomic status of some is yet to be finalised. There are presently 22 species of galaxiid recognised, but there are almost certainly more.

1.6.5 Recognition of New Diversity

In addition to all of the above, several new species unrelated to those just discussed have also been recognised from other geographical areas. A new species of *Neochanna* mudfish has been described, *N. heleioides* in Northland (Ling and Gleeson 2001). As well, two additional *Galaxias* species are recently described, both from the upper reaches of the Waitaki River/Mackenzie Basin and nearby waterways in the eastern, central South Island (McDowall and Waters 2002, 2003; Elkington and Charteris 2005). One of these, the lowland longjaw galaxias, *Gl. cobitinis* (Fig. 1.8), was long regarded as just a disjunct lowland isolate of an otherwise largely submontane upland longjaw species, *Gl. prognathus*, and I think it fair to say that it would probably not have been identified as distinct had the availability of molecular data not pointed to quite ancient separation of these two longjaw galaxias stocks. Much the same applies to the recognition and description of *Gl. macronasus* also from the same inland, submontane basin. Originally described from only a single location, this species, too, has since been found quite widely across the Mackenzie Basin (Elkington and Charteris 2005). In essence, molecular data have assisted with the taxonomic sorting of a series of populations, and have pointed to the unity/monophyly of populations of the newly recognised species.

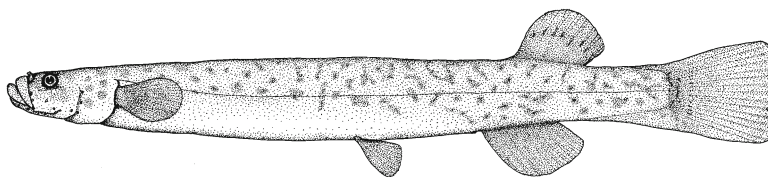


Fig. 1.8 Lowland longjaw galaxias, *Galaxias cobitinis*, 67 mm LCF (family Galaxiidae)

1.6.6 *Unresolved Problems in Gobiomorphus*

Further taxonomic problems related to ‘bullies’ of the genus *Gobiomorphus* (f. Eleotridae), remain unresolved. Studies of reproduction in captivity of Cran’s bully, *Gobiomorphus basalis*, showed that egg size differs between populations around Auckland in the northern North Island, and others around Wellington, in the south (author, unpubl. obs.). The taxonomic interpretation of this difference has yet to be made, but we could be looking at geographical variation within the species, or there may be more than one species involved. Also, genetic studies of upland bully, *Gobiomorphus breviceps* are revealing deep genetic dichotomies, and additional, undescribed taxa are almost certainly present (Smith et al. 2005; Stevens and Hicks 2009).

1.6.7 *The Arrival of Additional Species in New Zealand*

Additional species of fish have been recorded from New Zealand in recent decades that almost certainly relate to recent dispersal from elsewhere, probably eastern Australia. A third species of freshwater eel, the Australian spotted longfin eel *Anguilla reinhardtii*, began to appear in the rivers of northern New Zealand, probably in the last 20–25 years. This fish is apparently being brought to New Zealand by some presently unidentified shift in ocean currents to the north of New Zealand (Jellyman et al. 1996; McDowall et al. 1998), and this event was, I suspect, the first confirmed, historic, natural redistribution of a diadromous freshwater fish species in this way ever reported (though an anadromous Atlantic shad, *Alosa pseudoharengus* – f. Clupeidae, after having been successfully introduced to Californian rivers of the western seaboard of North America, is known to have spread across the northern Pacific Ocean to colonise river systems of northeastern Asiatic Pacific coasts – Whitehead 1985; McDowall 1988, 2003b). We cannot be sure that the spotted longfin will continue to recruit to New Zealand, and only time will tell whether this species becomes a permanent part of the country’s freshwater fish fauna.

However, Phillipps (1925) had recorded *A. reinhardtii* from New Zealand from the early decades of last century. This could have been a correct identification, though his record cannot be authenticated as there are no known voucher specimens. If Phillipps’ identification was correct, then *A. reinhardtii* might be arriving in New Zealand sporadically or episodically, and from time to time, for reasons that we do not understand. Given the very limited knowledge of the location of spawning in this eel, it is unlikely to be possible to determine the oceanographic events driving this dispersal of *A. reinhardtii*, and it may disappear from New Zealand waters as unexpectedly as it appeared.

In addition, two small estuarine gobioid fishes have recently been detected in northern locations, both also probably of Australian provenance. The dart goby, *Parioglossus marginalis* (f. Microdesmidae) (Fig. 1.9), was found in two locations in northern New Zealand in 2001 (McDowall 2001). Its place in the New Zealand

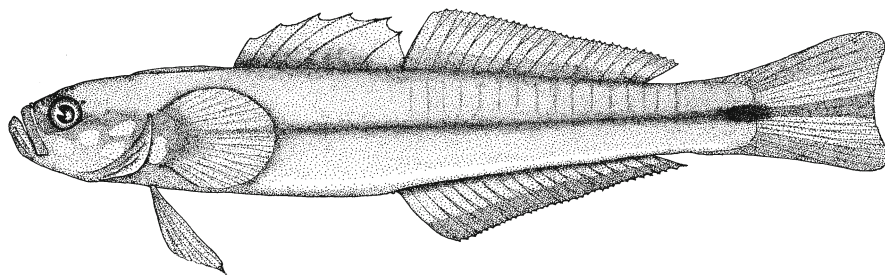


Fig. 1.9 Dart goby, *Parioglossus marginalis*, 43 mm TL (family Microdesmidae): a likely recent arrival in New Zealand fresh waters

freshwater fish fauna is uncertain. It may be largely estuarine, and could have come to New Zealand in ships' ballast; moreover it has not again been recorded so its long term establishment is uncertain. Much the same uncertainty applies to the even more recent report of *Gobiopterus semivestitus* (f. Gobiidae) also from northern New Zealand estuarine/fresh waters (McDowall and David 2008). It too may be primarily estuarine, may have come to New Zealand from Australia in ballast water, has been recorded only from a single estuary, and its persistence through a major flood event in the catchment involved is uncertain. The interest in all these records relates particularly to the processes involved in their arrival and their future place in lowland riverine and estuarine ecosystems in New Zealand, how far they may spread, and their potential survival and eventual possible firm establishment. If they are natural dispersals to New Zealand, they probably epitomise how the fish fauna of New Zealand has always been derived, as it has been augmented across geological time on an intermittent basis.

Taxonomic changes and discoveries over the past decade or two result in a view that New Zealand's indigenous freshwater fish fauna now comprises 38 species (see Table 1.1), giving an increase of 11 species, or more than 40%, in the past c. 20 years (McDowall 1990). Taken together, all of this understanding of the fauna's taxonomy and diversity, as well as good knowledge of the natural history of the fauna, and comprehensive knowledge of distributions (see below), means that a broad analysis of the fauna's biogeography is possible, timely, and of interest.

1.7 A Synopsis of the Present Fauna

More than half the species in the fauna, and most of the newly recognised taxonomic diversity, belong to the Galaxiidae (now 22 named species as well as the four presently undescribed lineages, discussed above – Table 1.1). This is a family that is widespread across southern cool-temperate latitudes of the earth: galaxiids are present in western and eastern Australia, Tasmania, New Caledonia, Lord Howe Island, New Zealand, the Chatham, Auckland, and Campbell Islands, Patagonian

South America, the Falkland Islands, and southern Africa (see Fig. 8.1). Thus the galaxiids give the appearance of having a distinctly Gondwanan range.

The next largest family is Eleotridae (seven species), the New Zealand species of which are allied to congeneric species in southeastern Australia (Thacker 2003; Thacker and Hardman 2005). The New Zealand Eleotridae have been shown to be a monophyletic sister clade to two Australian species of *Gobiomorphus* (Stevens and Hicks 2009). This group is clearly not Gondwanan, but has a heritage more widely in the Indo-West Pacific, and so displays a set of broad relationships distinctly different from the Galaxiidae, even though there is a commonality in that in both families there are congeneric Australian/New Zealand species.

There is also lesser representation in the New Zealand freshwater fish fauna from six further fish families: these include:

The southern pouched lamprey family Geotriidae, with one species shared by western Australia, eastern Australia, New Zealand, the Chatham Islands, Patagonian South America, and a dubious record from the Falkland Islands (McDowall et al. 2001); so, again, there is the appearance of a Gondwanan range.

The southern smelt family Retropinnidae (following Johnson and Patterson 1996), is found only in southeastern Australia, Tasmania, mainland New Zealand, and the Chatham Islands, with three New Zealand species in three genera (*Retropinna*, *Stokellia*, and *Prototroctes*) each with one New Zealand species. Though found only in Australia and New Zealand, retropinnids are most closely related to the Galaxiidae (McDowall 1969; Johnson and Patterson 1996) and these genera, too, should be regarded as representing a southern, perhaps Gondwanan, element.

Other families have distributions that resemble the Eleotridae in showing very much wider, ancestral, Indo-Pacific connections, including the freshwater eels (Anguillidae – 3 species in New Zealand) (see Fig. 7.2); and yet others, the weavers, or sandperches, f. Pinguipedidae, with the monotypic *Cheimarrichthys* in New Zealand fresh waters (see Fig. 7.5), and the largely southern *Rhombosolea* flounders, f. Pleuronectidae, also with a single species in New Zealand fresh waters. Both of these have their apparent closest affinities in the seas surrounding New Zealand (though both families Pinguipedidae and Pleuronectidae can be regarded as having more extensive Indo-Pacific ancestral connections (McDowall 1964b, 1973, 2002; McDowall and Whitaker 1975). Some ichthyologists place *Cheimarrichthys* in the monotypic family Cheimarrichthyidae (Pietsch 1989; Nelson 2006), but this does not materially alter our understanding of its relationships or biogeography: *Cheimarrichthys* has its closest relationships among the widespread, marine trachinoid fishes (Pietsch 1989), and is the only member of the group known from fresh waters.

Taking all of these patterns of relationship and diversity together, in a broad sense, the Australian-New Zealand connection is very strong (applying to all families in the freshwater fish fauna), but these connections represent two quite distinct groups of fish families: the Geotriidae, Galaxiidae and Retropinnidae are best viewed as southern cool-temperate groups, perhaps with connections to Gondwana, whereas the Anguillidae, Eleotridae, Pinguipedidae, and Pleuronectidae are Indo-Pacific groups with little or no indication of a Gondwanan connection. Thus although

the Australian-New Zealand parts of the distributions of the Anguillidae, Eleotridae, Pinguipedidae and Pleuronectidae appear similar to those of Galaxiidae, Geotriidae and Retropinnidae, their ancestral origins are quite different – and their evolutionary/biogeographical histories are also quite different, as well (McDowall 2002).

Perhaps, then, Australia-New Zealand should be seen as a nexus of two widespread freshwater fish faunas – one southern cool-temperate and giving the appearance of a classically Gondwanan group, the other Indo-Pacific and unrelated to any Gondwanan lineages. Cooper and Millener (1993) observed that “prevailing westerly winds and ocean currents have ensured that Australia has been the dominant source of immigrant species, especially in the late Cenozoic”, and this generalisation seems entirely applicable to the origins of the freshwater fish fauna (McDowall 1964b, 2002).

1.8 New Zealand Freshwater Fish Fossils

Fossils have a part to play in understanding historical biogeography insofar as they provide ancient information on what forms of fish were once present, and where they were distributed in past epochs – though absence of fossils does not equate to a former absence of taxa. Sometimes, too, fossils are valuable for understanding evolutionary history but they do not herald the earliest presence of the relevant groups in New Zealand so much as being their earliest known occurrence there.

The fossil freshwater fish fauna of New Zealand is quite sparse, and fish fossils have been reported from only a few general areas – the northeastern North Island, inland from Gisborne, and Central Otago. As a general statement, freshwater fish fossils so far discovered have all been associated with lacustrine deposits. This is not surprising as preservation of fossil material in rivers is far less likely. But it does mean that our knowledge of the fauna's diversity is likely to be strongly skewed towards lacustrine species. This is a distinct contrast with the modern freshwater fish fauna, which is heavily dominated by fluvial rather than lacustrine species. Most of the fish fossils are from central Otago in southern New Zealand. Most are galaxiids, and they are largely of Miocene age. As a result, what we know cannot be regarded as ‘representative’ of the fauna's history but only as some hints of what might once have been present here in past times.

The first report of freshwater fish fossils was by Oliver (1936), who described (though did not formally name) a galaxiid fossil from beds at Frasers Gully, near Kaikorai, Dunedin, Otago (and he thought they were Pliocene, but they are now thought to be c. 10 Ma and thus of Miocene age). Whitley (1956) later named this fossil as *Gl. kaikorai*, though I later suggested that this fossil, though not explicitly identifiable with any living form, could not be separated from a diversity of extant species, and therefore rejected use of the name. It perhaps most closely resembles *Gl. brevipinnis* and its recognition as a distinct species by Whitley was unjustified, especially given its lack of distinctive and diagnostic characters (McDowall 1976). Additional fossils were long ago recovered from the Foulden Hills, near

Middlemarch, in inland Otago (Fig. 1.10). These were said to resemble members of the *Galaxias vulgaris* species group (McDowall 1976). However a considerable additional amount of much better preserved material has more recently been found in the Foulden Hills deposit that provides a very different perspective on their nature and identity. This diatomite deposit is the site of an ancient marr lake, in which there are serial, probably annual layers of deposition of diatomaceous sediments from a small, very stable lake set in an old volcanic crater. Though probably c. 23 Ma, the deposit remains as well packed but unpetrified sediment that can be cut out of the consolidated deposit with an ordinary chainsaw, lifted away and peeled apart, layer by layer (Fig. 1.11). The fish lie between the layers in this deposit which, in total, may cover a period of many thousands of years. The deposit also includes numerous plant leaves, other plant parts including fruit, pollen-bearing flowers, leaf fungi, diatoms and insect parts (Lee et al. 2006). Of particular, present relevance is a large and remarkably well-preserved fossil, including quite exquisite detail of the vertebral column and associated bones, and also the fins (Fig. 1.10). This shows that the fish from this site are quite distinct, with very expansive dorsal and anal fins, and tail, and the fossils from this deposit were formally described as the distinct species *Gl. effusus* by Lee et al. (2007). Further studies of this deposit are underway by geologists, and will be followed with interest!

A further, rather larger *Galaxias* fossil fragment, perhaps derived from an individual fish possibly 383 mm long, was reported from near Bannockburn in Central Otago (McDowall and Pole 1997). It is also from the Miocene, and is quite unlike any living species, but insufficient detail has been preserved to permit formal description. Additional material from other early Miocene formations at Bannockburn, Central Otago deposits was reported by Lee et al. (2007) and again, distinct taxa are likely to have been involved though again insufficient detail is present to permit formal description. These latter fossils come from what has been described as Palaeo-lake Manuherikia, a very extensive lake or lake complex that once existed in the area (Douglas 1986; Craw and Norris 2003) that may have



Fig. 1.10 *Galaxias effusus* (family Galaxiidae), a recently described Miocene fossil species from southeastern New Zealand (photo: D.E. Lee)

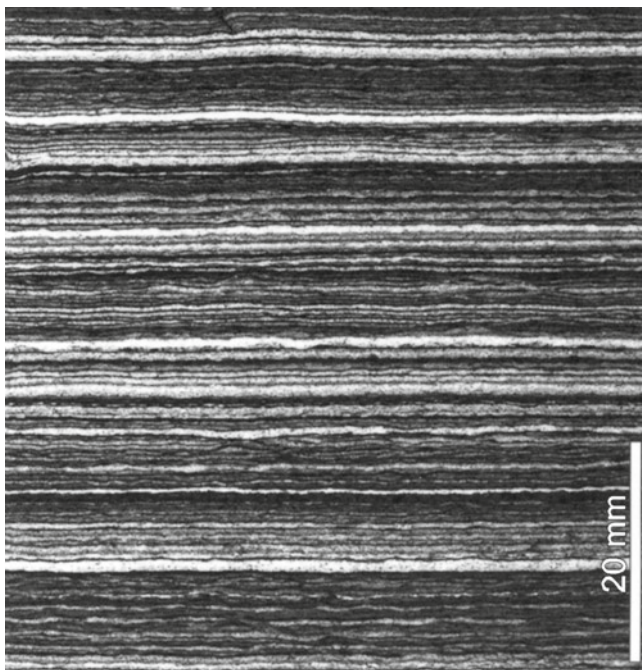


Fig. 1.11 Laminated dark and light diatomite couplets deposited in the bed of a small marr lake, c. 1 km in diameter, Foulden Hills Diatomite, Middelmarsh, New Zealand, from which the fossil in figure 10 was obtained (photo: J.K. Lindqvist)

extended to as much as 5600 km². Lee et al. (2007) also described but did not formally name additional material from these deposits, though there seem to be at least two species present, some of them relatively large for a galaxiid, perhaps as large as 500 mm long (Lee et al. 2007); by comparison, the largest known extant species of *Galaxias* is known to reach 580 mm and few species exceed 300 mm (Clarke 1899; McDowall 1990).

McDowall and Lee (2005) also reported on two scale fragments from other Miocene deposits, also near Bannockburn (Fig. 1.12). Though only about 1 ½ scales were recovered, there is enough present to show that they certainly belonged to some group of fishes not otherwise recorded from New Zealand fresh waters, past or present. They bear a close resemblance to scales from Australian freshwater percichthyids (Fig. 1.13), the Australian ‘basses and cods’ (Harris and Rowland 1996), and so they are of especial biogeographical significance as they reveal an entirely distinct group of fishes that was once living in New Zealand in Miocene times. Though providing the least amount of preserved morphological material, these two scale fragments rank as the most intriguing freshwater fish fossils found in New Zealand, to date, at least in terms of the group that they represent.

Some additional Otago fossil freshwater fish material can be identified as being gobioid in origin (McDowall et al. 2006b) (Fig. 1.14), identification being primarily

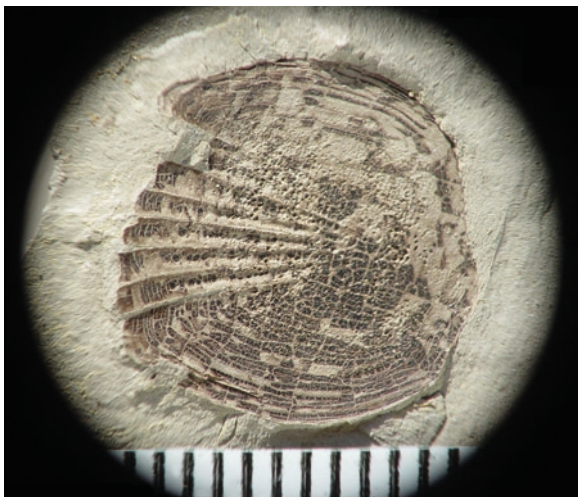


Fig. 1.12 Fossil scale from a likely lower perciform fish from Miocene Bannockburn deposit, Central Otago, New Zealand (photo: J.K. Lindqvist) (scale shows millimetres)

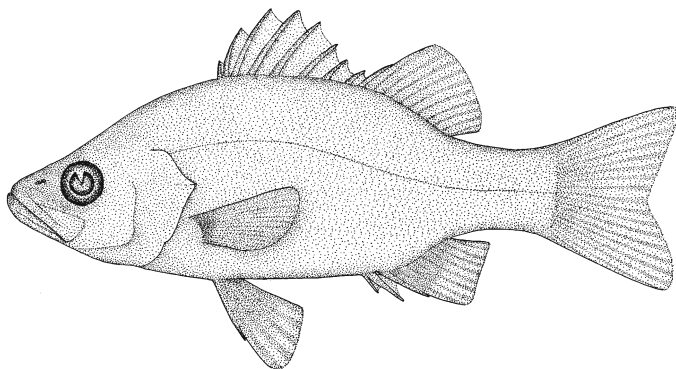


Fig. 1.13 Australian estuary perch, *Macquaria colonorum*, 240 mm LCF (family Percichthyidae): perhaps like the fish from which the scale in figure 12 originated

from very distinctive detail in scale traces (Fig. 1.15). Positions of the various fin traces in these fossils, their low vertebral counts, and other details, are also consistent with these fishes being gobioids, and these fossils are presumed to be of the same general type as extant New Zealand species of *Gobiomorphus* (see Fig. 1.7). They are of particular interest from that perspective, showing that there have been fish of this general type in New Zealand freshwater for a very long time, perhaps for as many as 20 million years.

A substantial, additional amount of fish skeletal remains has been recovered from sediments, possibly from the same general palaeolake system at both St Bathans (now referred to as the St Bathans fauna – Worthy and Lee 2008) that

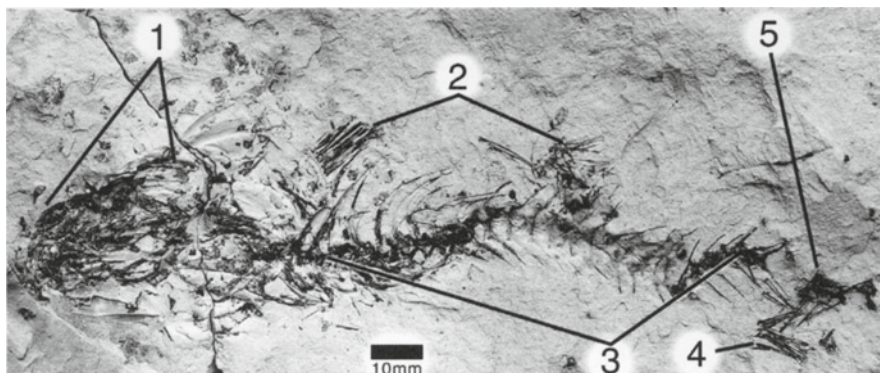


Fig. 1.14 Carbonised fossil trace of a likely species of eleotrid from Miocene deposit, near Fiddlers Flat, Central Otago, not unlike modern species of *Gobiomorphus* (family Eleotridae): 1: jumble of cranial bones; 2: groups of fin rays, those to left probably pectoral fin and those to right a dorsal fin; 3: vertebral column; 4: caudal fin rays; 5: possible hypural/caudal assemblage (photo: J.K. Lindqvist)

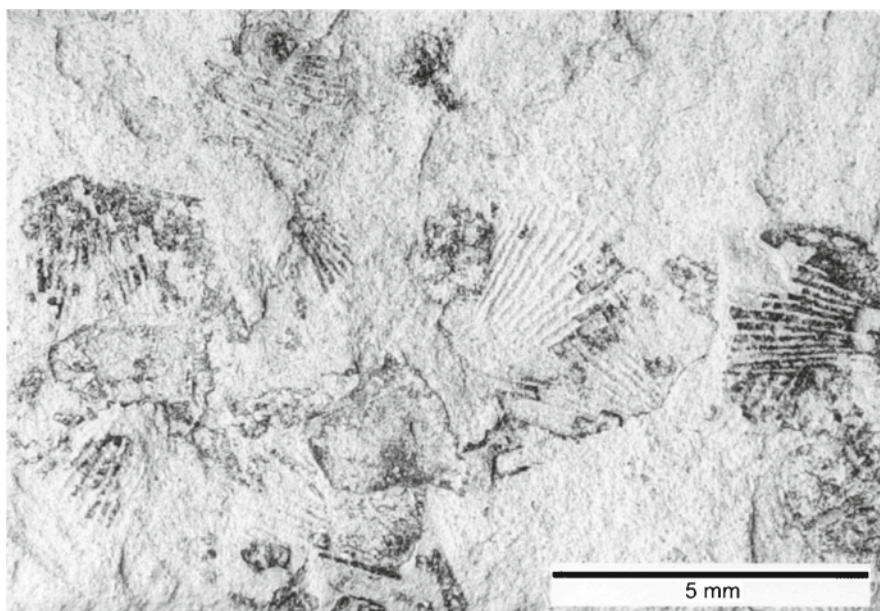


Fig. 1.15 Highly characteristic eleotrid-like fossil scale traces/imprints from the Miocene deposit from which the fossil in figure 14 was obtained (photo: J.K. Lindqvist)

at present defy identification. There are large numbers of totally disarticulated fish bones, often rather abraded, and some of these skeletal fragments could easily belong to the same group of fishes as the two Bannockburn scales. These lower perciform fishes tend to be very generalised and to lack distinctive or idiosyncratic

characters that might facilitate identification, so that it is perhaps not surprising that identifying these totally disarticulated fragments, probably wave washed along a lake shore, has proved difficult.

Based on molecular studies, Stevens and Hicks (2009) dated the presence of basal eleotrids in New Zealand back into Miocene times, and so they are estimated, from genetic studies, as being about the same age as the earliest known gobioid fossils.

All of these fossil fish traces from Otago are part of a very substantial fauna and flora being discovered in the area, particularly including a highly diverse and well-preserved fossil flora of Miocene age (Pole et al. 2003). No doubt, substantial additional discoveries are yet to emerge from a quite extensive area, but it is clear that there was a diverse aquatic and wetland/lake-related animal community in these waters in Miocene times. Feldman and Pole (1994) have described a freshwater crayfish of the genus *Paranephrops* (f. Parastacidae) from the same general lake system, and Molnar and Pole (1997) have identified a crocodile. In addition, there is a high diversity of aquatic and wetland bird fossils from much the same general deposits (Worthy and Holdaway 2002; Worthy and Lee 2008, Worthy et al. 2007). Worthy et al. (2006) recorded the first known non-volant, terrestrial mammalian fossil from New Zealand, which was found in the same general area. Precisely what kind of mammal was involved remains uncertain. A purported snake from the same general area and period (Worthy et al. 2002) has since been discounted. Most recently Jones et al. (2009) described a jaw fragment from a rhynchocephalian (or sphenodontid) of much the same age, and thus a very early fossil related to the extant tuatara, *Sphenodon*. There is a mass of additional unstudied fish material, mostly otoliths and bone fragments from mudstone deposits in Central Otago, which awaits study; its identification probably won't be easy, but it could be from the same group of fishes represented by the scales, discussed above.

So little can be determined from most of the various fish fossils that their affinities with extant forms cannot be determined with any clarity or certainty, and so they are not highly informative phylogenetically. What they do provide, however, is evidence that there was diversity of freshwater fishes in southern New Zealand in Miocene times, with some of that diversity being no longer recognised in the extant fauna. This might be no surprise to those who link galaxiids to Gondwana, though an explicit Gondwana ancestry of the galaxiids cannot be assumed. Perhaps a little more interesting is the fact that there were probable eleotrid fossils, from Central Otago at about that time; if that identification is accepted, it means that eleotrids were already present there in the mid-Cenozoic, perhaps as early as anywhere in the world (Romer 1966), and so they are of some wider significance. The percichthyid is totally novel for New Zealand (McDowall and Lee 2005): there is no other published hint of this group in fresh waters there.

Fossil traces of an eleotrid were also long ago reported from what were given as Late Pliocene or Pleistocene lacustrine deposits at Waipaoa, in the northeastern North Island (not far from Gisborne), by Oliver (1928). They are now regarded as of Pleistocene age (Kennedy and Alloway 2004; Kennedy et al. 2008), and so are quite young and not of major interest. There is more recently-collected material from this area that is also clearly eleotrid, especially including distinctive scale impressions that facilitate identification (Fig. 1.15) (McDowall et al. 2006b). Also

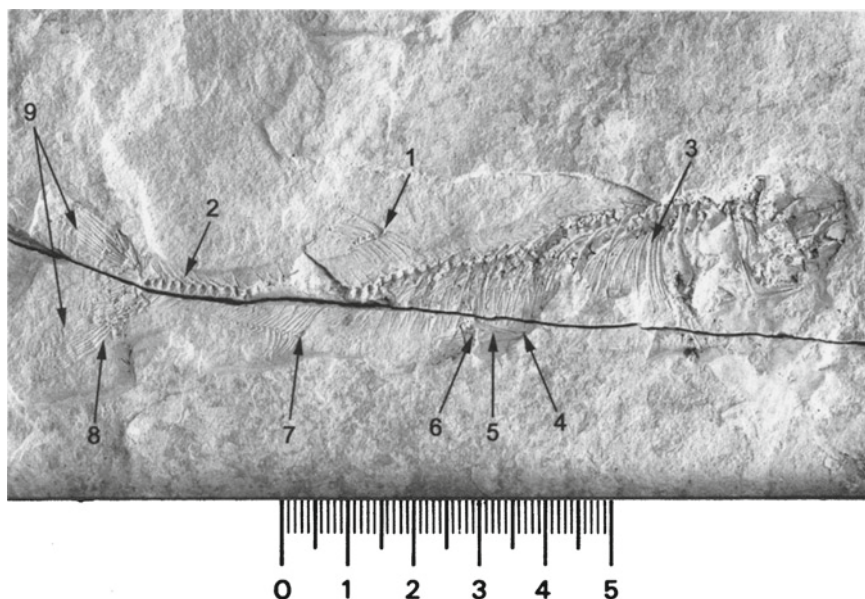


Fig. 1.16 Fossil New Zealand grayling, *Prototroctes*, from Waipaoa Valley, northeastern North Island, Pleistocene in age: 1: origin of dorsal fin; 2: flattened caudal neural spines; 3: ribs; 4: anterior pelvic symphysis; 5: paired pelvic bones; 6: pelvic fin rays; 7: origin of anal fin; 8: Distinctly flattened bounding rays in caudal fin; 9: upper caudal fin rays of a probably forked caudal fin (photo: E.M. Kennedy)

from the same general area and age are two partial skeletons of the New Zealand grayling, *P. oxyrhynchus* (Fig. 1.16) (McDowall et al. 2006a), which became extinct in the early decades of the twentieth century (McDowall 1990).

References

- Allibone RM (1999) Impoundment and introductions: their impacts on native fish of the upper Waipori River. *New Zealand J R Soc N Z* 29:291–299
- Allibone RM, McDowall RM (1997) Conservation ecology of the dusky galaxias, *Galaxias pullus* (Teleostei: Galaxiidae). *N Z Cons Sci Publ* 6:1–48
- Allibone RM, Townsend CR (1997a) Distribution of four recently discovered galaxiid species in the Taieri River, New Zealand: the role of microhabitat. *J Fish Biol* 51:1235–1246
- Allibone RM, Townsend CR (1997b) Reproductive biology, species status and taxonomic relationships of four recently discovered galaxiid fishes in a New Zealand river. *J Fish Biol* 51:1247–1261
- Allibone RM, Townsend CR (1998) Comparative dietary analysis of a recently described fish species complex (Galaxiidae) in a New Zealand river. *N Z J Mar Freshwater Res* 32:351–361
- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Allibone RM, Crowl TA, Holmes JM, King TM, McDowall RM, Townsend CR, Wallis GP (1996) Isozyme analysis of *Galaxias* species (Teleostei: Galaxiidae) from the Taieri River, South Island, New Zealand: a species complex revealed. *Biol J Linn Soc* 57:107–127

- Avice J (2009) Phylogeography: retrospect and prospect. *J Biogeogr* 36:3–15
- Barker JM, Lambert DM (1988) A genetic analysis of populations of *Galaxias maculatus* from the Bay of Plenty: implications for natal river return. *N Z J Mar Freshwater Res* 22:321–326
- Begg AC, Begg NC (1969) James Cook and New Zealand. Government Printer, Wellington, N Z, 158 pp
- Bloch ME, Schneider JG (1801) *Systema Ichthyologiae*. Sanderiano, Berlin, Germany, 514 pp
- Burnet AMR (1959) Electric fishing with pulsatory direct current. *N Z J Sci* 2:46–56
- Clarke FE (1899) Notes on New Zealand Galaxiidae, more especially those of the western slopes: with descriptions of new species. *Trans Proc N Z Inst* 31:78–91
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Cranfield HJ (1962) *Studies on the systematics of Gobiomorphus gobioides (Cuvier and Valenciennes)*. Unpublished MSc Thesis, University of Canterbury, Christchurch, N Z, 240 pp
- Craw D, Norris RJ (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago, Dunedin, N Z, pp 17–34
- Crow SK, Waters JM, Closs GP, Wallis GD (2009) Morphological and genetic analysis of *Galaxias* 'southern' and *G. gollumoides*: interspecific differentiation and intraspecific structuring. *J R Soc N Z* 29:43–62
- Cuvier G, Valenciennes A (1837) *Histoire Naturelle des Poissons* 12:247–250
- Darlington PJ (1957) *Zoogeography: the geographical distribution of animals*. Wiley, New York, 675 pp
- Darwin C (1859) *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray, London, 502 pp
- Dijkstra LH, Jellyman DJ (1999) Is the subspecies classification of the freshwater eels *Anguilla australis australis* Richardson and *A. australis schmidtii* Phillipps still valid? *Mar Freshwater Res* 50:261–263
- Douglas BJ (1986) Lignite resources of Central Otago, Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessment and exploration models. *N Z Energy Res Devel Comm Publ*. 2 vols
- Elkington SP, Charteris SC (2005) Freshwater fish of the upper Waitaki Valley. Department of Conservation, Christchurch, N Z, 44 pp
- Esa YB, Waters JM, Wallis GP (2001) Introgressive hybridization between *Galaxias depressiceps* and *Galaxias* sp. D (Teleostei: Galaxiidae) in Otago, New Zealand: secondary contact mediated by water races. *Conserv Genet* 1:329–339
- Feldman RM, Pole M (1994) A new species of *Paranephrops* White, 1842 a fossil decapod crayfish (Decapoda: Parastacidae) from the Manuherikia Group (Miocene) Central Otago, New Zealand. *N Z J Geol Geophys* 37:163–167
- Gleeson DM, Howitt RLJ, Ling N (1999) Genetic variation, population structure and cryptic species within the black mudfish, *Neochanna diversus*, an endemic galaxiid from New Zealand. *Mol Ecol* 8:47–57
- Gmelin JF (1789) *Systema naturae*, 6 vols, 13th edn. Lichenstein, Lipsiae, Germany
- Gray JE (1842) Three hitherto unrecorded species of freshwater fish brought from New Zealand and presented to the British Museum by Dr Dieffenbach. In: Gray JE (ed) *The zoological miscellany*. Trentell, Wurtz, London, p 73
- Günther A (1967) On a new form of mudfish from New Zealand. *Ann Mag Nat Hist* 3:305–309
- Günther A (1870) Notes on *Prototroctes*, a fish from fresh waters of the Australian region. *Proc Zool Soc Lond* 1870:150–152
- von Haast J (1873) Notes on some undescribed fishes of New Zealand. *Trans Proc N Z Inst* 5:272–278
- von Haast J (1874) On *Cheimarrichthys fosteri*, a new genus belonging to the New Zealand freshwater fishes. *Trans Proc N Z Inst* 6:103–104

- Harris JH, Rowland SJ (1996) Australian freshwater cods and basses. In: McDowall RM (ed) Freshwater fishes of southeastern Australia. Reed, Sydney, NSW, Australia, pp 150–163
- Hector J (1871) On the Salmonidae of New Zealand. Trans Proc N Z Inst 3:133–136
- Hutton FW (1873) Contributions to the ichthyology of New Zealand. Trans Proc N Z Inst 5:259–272
- Jellyman DJ, Dijkstra LH, Chisnall BL, Boubée JAT (1996) The first record of the Australian longfinned eel, *Anguilla reinhardtii*, in New Zealand. Mar Freshwater Res 47:1037–1040
- Jenyns L (1842) Fish. In: Darwin C (ed) The zoology of the voyage of HMS Beagle 4:1–172. Smith Elder, London
- Johnson GD, Patterson C (1996) Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic, New York, pp 251–332
- Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and the palaeobiogeography of the tuatara (*Sphenodon*). Proc R Soc Lond B Biol Sci 276:1385–1390
- Kennedy EM, Alloway BV (2004) Paleoclimate assessment, paleobotany and stratigraphy of a mid-Pleistocene lacustrine section, Ormond Valley, Gisborne. IGNS Sci Rep 2004(13):1–32
- Kennedy EM, Alloway BV, Mildenhall DC, Cochran U, Pillans BV (2008) An integrated terrestrial paleoenvironmental record from the mid-Pleistocene transition, eastern North Island, New Zealand. Quatern Internat 178:146–166
- King M (2007) The Penguin history of New Zealand illustrated. Penguin, Auckland, N Z, 563 pp
- King TM, Wallis GP (1998) Fine scale genetic structuring in endemic galaxiid fish populations of the Taieri River. N Z J Zool 25:17–22
- Lee DE, Bannister JM, Lindqvist JK (2006) Fossil flowers, fruit, leaves, diatoms, sponges, fish and insects from a Central Otago lake deposit: a diverse, 20 million year old forest lake ecosystem. Geol Soc N Z Misc Publ 121:22–24
- Lee DE, McDowall RM, Lindqvist JK (2007) *Galaxias* fossils from Miocene Lake deposits, Central Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). J R Soc N Z 37:109–130
- Ling N, Gleeson DM (2001) A new species of mudfish, *Neochanna* (Teleostei: Galaxiidae) from northern New Zealand. J R Soc N Z 31:385–392
- Maitland PS, Campbell RN (1992) Freshwater fishes of the British Isles. Harper Collins, London, 368 pp
- Matsuura K, Doi A, Shinohara G (2000) Distribution of freshwater fishes in Japan: supplement to catalog of the freshwater fish collection in the National Science Museum. Tokyo, National Science Museum, Tokyo, Japan, 256 pp
- Mayr E (1942) Systematics and the origin of species - from the viewpoint of a zoologist. Columbia University, New York, 334 pp
- McDowall RM (1964a) A redescription of the freshwater red-finned bully, *Gobiomorphus huttoni* (Ogilby). Trans R Soc N Z Zool 3:3–15
- McDowall RM (1964b) The affinities and derivation of the New Zealand fresh-water fish fauna. Tuatara 12:59–67
- McDowall RM (1965) Descriptive and taxonomic notes on *Grahamichthys radiatus* (Valenciennes), Eleotridae. Trans R Soc N Z Zool 7:51–56
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. Copeia 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. Bull Mus Comp Zool Harv Univ 139:341–431
- McDowall RM (1971) The identity of *Eleotris radiata* Valenciennes (Pisces: Eleotridae). Copeia 1971:731–732
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). J R Soc N Z 2:325–367
- McDowall RM (1973) Relationships and taxonomy of the New Zealand torrentfish, *Cheimarrichthys fosteri* Haast (Pisces: Mugiloididae). J R Soc N Z 3:199–217

- McDowall RM (1975a) Gerald Stokell's "Freshwater and diadromous fishes of New Zealand" in the context of his other published works, with a bibliography of his publications. *J R Soc N Z* 5:219–223
- McDowall RM (1975b) A revision of the New Zealand species of *Gobiomorphus* (Pisces: Eleotridae). *Natl Mus N Z Rec* 1:1–32
- McDowall RM (1976) Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J R Soc N Z* 6:17–22
- McDowall RM (1988) Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London, 309 pp
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1994a) Gamekeepers for the nation: the story of New Zealand's acclimatisation societies, 1861–1990. Canterbury University Press, Christchurch, N Z, 512 pp
- McDowall RM (1994b) The Tarndale bully, *Gobiomorphus alpinus* (Pisces: Eleotridae) revisited and redescribed. *J R Soc N Z* 24:117–124
- McDowall RM (1997) Two further new species of *Galaxias* (Teleostei: Galaxiidae) from the Taieri River, southern New Zealand. *J R Soc N Z* 27:199–217
- McDowall RM (2000a) The Reed field guide to New Zealand freshwater fishes. Reed, Wellington, N Z, 224 pp
- McDowall RM (2000b) Gerald Stokell – 1890–1972: horticulturalist, ichthyologist. *Dictionary N Z Biog* 5:499–500
- McDowall RM (2001) *Parioglossus* (Teleostei: Microdesmidae) in New Zealand. *N Z J Mar Freshwater Res* 35:165–172
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2003a) Variation in vertebral number in galaxiid fishes (Teleostei: Galaxiidae): a legacy of life history, latitude and length. *Environ Biol Fish* 66:361–381
- McDowall RM (2003b) Shads and diadromy: implications for ecology, evolution and biogeography. In: Limburg KA, Waldman JR (eds) Status and conservation of the world's shads. *Am Fish Soc Symp* 35:11–23
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McDowall RM (2006) The taxonomic status, distribution and identification of the *Galaxias vulgaris* species complex in the eastern/southern South Island and Stewart Island. NIWA Client Rep CHCDOC2006-081:1–40
- McDowall RM (2008) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM (in press) Ikawai: freshwater fishes in Maori culture and economy. Canterbury University Press, Christchurch, N Z
- McDowall RM, Allibone RM (1994) Possible competitive exclusion of common river galaxias (*Galaxias vulgaris*) by koaro (*G. brevipinnis*) following impoundment of the Waipori River, Otago, New Zealand. *J R Soc N Z* 24:161–168
- McDowall RM, Chadderton WL (1999) *Galaxias gollumoides* (Teleostei: Galaxiidae), a new fish species from Stewart Island, with notes on other non-migratory freshwater fishes present on the island. *J R Soc N Z* 29:77–88
- McDowall RM, David BO (2008) *Gobiopterus* in New Zealand (Teleostei: Gobiidae) with observations on sexual dimorphism. *N Z J Mar Freshwater* 42:325–331
- McDowall RM, Hewitt J (2004) Attempts to distinguish morphotypes in the Canterbury-Otago non-migratory *Galaxias* species complex. *DOC Sci Internal Ser* 165:1–18
- McDowall RM, Lee DE (2005) Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *J R Soc N Z* 35:339–344
- McDowall RM, Pole M (1997) A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J R Soc N Z* 27:193–198
- McDowall RM, Stevens MI (2007) Taxonomic status of the Tarndale bully *Gobiomorphus alpinus* (Teleostei: Eleotridae), revisited – again. *J R Soc N Z* 37:15–29

- McDowall RM, Wallis GP (1996) Description and redescription of *Galaxias* species (Teleostei: Galaxiidae) from Otago and Southland. J R Soc N Z 26:401–427
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. N Z J Zool 29:41–52
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. J R Soc N Z 33:675–691
- McDowall RM, Whitaker AH (1975) The freshwater fishes. In: Kuschel G (ed) Biogeography and ecology in New Zealand. Monogr Biol 27:277–299
- McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands freshwater fishes. Aquatic Conserv Mar Freshwater Ecosyst 11:473–486
- McDowall RM, Jellyman DJ, Dijkstra LH (1998) Arrival of an Australian anguillid eel in New Zealand: an example of transoceanic dispersal. Environ Biol Fishes 51:1–6
- McDowall RM, Kennedy EM, Alloway BV (2006a) A fossil southern grayling, genus *Prototroctes* (Teleostei: Retropinnidae), from the Pleistocene of northeastern New Zealand. J R Soc N Z 36:27–36
- McDowall RM, Kennedy EM, Lindqvist JK, Lee DE, Gregory MR (2006b) Probable *Gobiomorphus* fossils from the Miocene and Pleistocene of New Zealand (Teleostei: Eleotridae). J R Soc N Z 36:97–109
- Mitchell CP (1995) A new species of *Galaxias* (Pisces: Galaxiidae) from Chatham Island, New Zealand. J R Soc N Z 25:89–93
- Mitchell CP, Scott D (1979) Muscle myogens in the New Zealand Galaxiidae. N Z J of Mar Freshwater Res 2:285–294
- Molnar RE, Pole M (1997) A Miocene crocodile from New Zealand. Alcheringa 21:65–70
- Myers GS (1938) Fresh-water fishes and West-Indian zoogeography. Smithsonian Rep 1937:339–364
- Myers GS (1949) Salt tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdr Dierk 28:315–322
- Myers GS (1951) Fresh-water fishes and East Indian zoogeography. Stanf Ichthyol Bull 4:11–21
- Nelson JS (2006) Fishes of the world 4th ed. Wiley, New York, 601 pp
- Ogilby JD (1894) Description of five new fishes from the Australasian region. Proc Linn Soc NSW 9(2):374
- Oliver WRB (1928) The flora of the Waipaoa series (later Pliocene) of New Zealand. Trans Proc N Z Inst 59:287–303
- Oliver WRB (1936) The Tertiary flora of the Kaikorai Valley, Otago, New Zealand. Trans Proc R Soc N Z 66:284–304
- Phillipps WJ (1919) Life history of the fish *Galaxias attenuatus*. Aust Zool 1:211–213
- Phillipps WJ (1923a) The New Zealand smelt, *Retropinna retropinna*. N Z J Sci Technol 6:166–167
- Phillipps WJ (1923b) Note on the occurrence of the New Zealand mudfish or hauhou (*Neochanna apoda*). N Z J Sci Tech 6:62–63
- Phillipps WJ (1924a) The New Zealand minnow. N Z J Sci Tech 7:117–119
- Phillipps WJ (1924b) The koaro: New Zealand's subterranean fish. N Z J Sci Tech 7:190–191
- Phillipps WJ (1925) New Zealand eels. N Z J Sci Tech 8:28–30
- Phillipps WJ (1926) New or rare fishes of New Zealand. Trans Proc N Z Inst 56:529–537
- Phillipps WJ (1929) Notes on the fresh-water papanoko (*Cheimarrichthys fosteri* Haast). N Z J Sci Tech 11:166–168
- Phillipps WJ (1940) The fishes of New Zealand. Avery, New Plymouth, N Z, 87 pp
- Pietsch TW (1989) Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989:253–303
- Pole M, Douglas B, Mason G (2003) The terrestrial Miocene biota of southern New Zealand. J R Soc N Z 33:415–426
- Regan CT (1905) A revision of the fishes of the family Galaxiidae. Proc R Soc, London 2:363–384
- Richardson J (1848) Ichthyology of the voyage of the HMS *Erebus* and *Terror*. In: The voyage of HMS. *Erebus* and *Terror*. Janson, London, 139 pp
- Romer AS (1966) Vertebrate paleontology. University of Chicago, Chicago, IL, 468 pp

- Sauvage MHE (1880) Notice sur quelques poissons de l'Isle Campbell et de l'Indo China. Bull Soc Philom Paris 4(7):228–234
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tarndale bully revisited with molecular markers: an ecophenotype of the common bully, *Gobiomorphus cotidianus* (Pisces: Gobiidae). J R Soc N Z 33:663–673
- Smith PJ, McVeagh SM, Allibone RM (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. J Fish Biol 67:627–639
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. Evol Ecol Res 11:109–123
- Stokell G (1928) Report on preliminary examination of trout scales and stomachs. Ann Rep N Canterbury Acl Soc 64:4
- Stokell G (1936) The nematode parasites of Lake Ellesmere trout. Trans R Soc N Z 66:80–96
- Stokell G (1938a) The ill-conditioned trout present in the lower Selwyn during the spring of 1932. Trans R Soc N Z 68:380–389
- Stokell G (1938b) A new species of *Galaxias* with a note on the second occurrence of *Galaxias burrowsii* Phillipps. Rec Canterbury Mus 4:203–208
- Stokell G (1939) A new freshwater fish of the genus *Philypnodon*. Trans Proc R Soc N Z 69:129–133
- Stokell G (1941a) A revision of the genus *Retropinna*. Rec Canterbury Mus 4:361–372
- Stokell G (1941b) A revision of the genus *Gobiomorphus*. Trans R Soc N Z 70:361–372
- Stokell G (1945) The systematic arrangement of the New Zealand Galaxiidae. Part I. Generic and sub-generic classification. Trans R Soc N Z 75:124–137
- Stokell G (1949a) A freshwater smelt from the Chatham Islands. Rec Canterbury Mus 5:205–207
- Stokell G (1949b) The systematic arrangement of the New Zealand Galaxiidae. Part II. Specific classification. Trans R Soc N Z 77:472–496
- Stokell G (1954) Contributions to galaxiid taxonomy. Trans R Soc N Z 82:411–418
- Stokell G (1955) Freshwater fishes of New Zealand. Simpson & Williams, Christchurch, N Z, 145 pp
- Stokell G (1959) Notes on galaxiids and eleotrids with descriptions of new species. Trans Proc R Soc N Z 87:265–269
- Stokell G (1960) The validity of *Galaxias postvectis* Clarke, with notes on other species. Rec Dominion Mus 3:235–239
- Stokell G (1962) A new species of *Gobiomorphus*. Trans R Soc N Z Zool 2:32–34
- Stokell G (1966) A preliminary investigation of the systematics of some Tasmanian Galaxiidae. Pap Proc R Soc Tasm 100:73–79
- Thacker CE (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). Mol Phylogen Evol 26:354–368
- Thacker CE, Hardman MA (2005) Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidei). Mol Phylogen Evol 37:858–871
- Wallis GP, Waters JM (2003) The phylogeography of southern galaxiid fishes. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) The natural history of southern New Zealand. Otago University Press, Dunedin, N Z, pp 101–104
- Wallis GP, Judge KF, Bland J, Waters JM, Berra TM (2001) Genetic diversity in New Zealand *Galaxias vulgaris* sensu lato (Teleostei: Osmeriformes: Galaxiidae): a test of a biogeographic hypothesis. J Biogeogr 28:59–67
- Waters JM, McDowall RM (2005) Phylogenetics of the Tasmanian and New Zealand mudfishes: evolution of an eel-like body plan. Mol Phylogen Evol 37:417–425
- Waters JM, Wallis GP (2000) Across the Southern Alps by river capture? Freshwater fish phylogeography in South Island, New Zealand. Mol Ecol 9:1577–1582
- Waters JM, Wallis GP (2001a) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. J Fish Biol 58:1166–1180

- Waters JM, Wallis GP (2001b) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Esa YB, Wallis GP (1999) Characterization of microsatellite loci from a New Zealand freshwater fish (*Galaxias vulgaris*) and their potential for analysis of hybridization in Galaxiidae. *Mol Ecol* 8:1080–1082
- Waters JM, Dijkstra LH, Wallis GP (2000a) Biogeography of a Southern Hemisphere freshwater fish: how important is dispersal? *Mol Ecol* 9:1851–1821
- Waters JM, Esa YB, Wallis GP (2001a) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298
- Waters JM, Craw D, Youngson JH, Wallis GP (2001b) Genes meet geology: fish phylogeographic pattern reflects ancient rather than modern drainage patterns. *Evolution* 55:1844–1855
- Waters JM, Lopez JA, Wallis GP (2000b) Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthys: Galaxiidae): dispersal, vicariance and the place of *Lepidogalaxias salamandroides*. *Syst Biol* 49:777–795
- Whitehead PJP (1985) Clupeoid fishes of the world (suborder Clupeoidei): an annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf herrings. Part 1. Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synop* 125:1–303
- Whitley GP (1956) New fishes from Australia and New Zealand. *Proc R Zool Soc N S W* 1954–55:34–38
- Whitley GP, Phillipps WJ (1939) Descriptive notes on some New Zealand fishes. *Trans Proc N Z Inst* 69:228–236
- Worthy TH, Holdaway RN (2002) *The lost world of the moa*. Canterbury University Press, Christchurch, N Z, 718 pp
- Worthy TH, Lee MSY (2008) Affinities of Miocene waterfowl (Anatidae: *Manuherikia*, *Dunstanetta* and *Miotadorna*) from the St Bathans fauna, New Zealand. *Palaeontology* 51:677–801
- Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD (2006) Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, south-west Pacific. *Proc Nat Acad Sci* 103:19419–19423
- Worthy TH, Tennyson ADJ, Jones C, McNamara JA (2002) A diverse Early-Miocene (15–20 Ma) terrestrial fauna from New Zealand reveals snakes and mammals. *IPC2002 Geol Soc Abstr* 68:174–175
- Worthy TH, Tennyson AJD, Jones C, McNamara JA, Douglas BJ (2007) Miocene waterfowl and other birds from Central Otago, New Zealand. *J Syst Palaeontol* 5:1–39

Chapter 2

The Geographical Setting of New Zealand and Its Place in Global Geography

Abstract New Zealand has three main islands and many smaller ones at mid-temperate latitudes, steep topography and many rivers, mostly flowing east or west, with hard rock gravels, and many lakes, all of them young and most of them either volcanic (North Island) or glacial (South Island). Early biogeographers were Charles Darwin and Alfred Wallace, with strong interest from local biogeographers from the late nineteenth century, particularly palaeontologist Charles Fleming. The New Zealand freshwater fish fauna has derivations from diadromous species that can disperse across oceans and around the coastline. The advent of plate tectonics profoundly influenced biogeography through the last half of the twentieth century, but it is uncertain whether this has had any implications for the derivation of the freshwater fish fauna, a topic that has been highly controversial.

Keywords Alfred Wallace • Charles Fleming • Charles Darwin • Diadromy • Dispersal • History • Gondwana • History • Plate tectonics

2.1 New Zealand's Global Setting

New Zealand (Fig. 2.1) is a slender archipelago tucked away in the temperate southwestern Pacific Ocean (see Fig. 1.1), in a sense forming a land boundary between that huge ocean to the east and the Tasman Sea to the west; it ranks as about the largest/most isolated group of islands globally, with area around 268,000 km², and positioned c. 2,000 km east of southern Australia, some 6,000 km west of Patagonian South America, and 4,000 km north of Antarctica. To the north and east of New Zealand is the vast Pacific Ocean with its scattered groups of tiny, often volcanic, oceanic islands, most of them much more tropical than New Zealand. Some oceanic islands are more remote than New Zealand but are much smaller in area, such as Hawaii (c. 17,000 km²), while others are larger but far less remote such as Madagascar (587,000 km²) or Borneo (c. 745,000 km²). No island as large or larger than New Zealand is anywhere near as remote, nor is any such remote island anywhere near as big as New Zealand. In position and area New Zealand

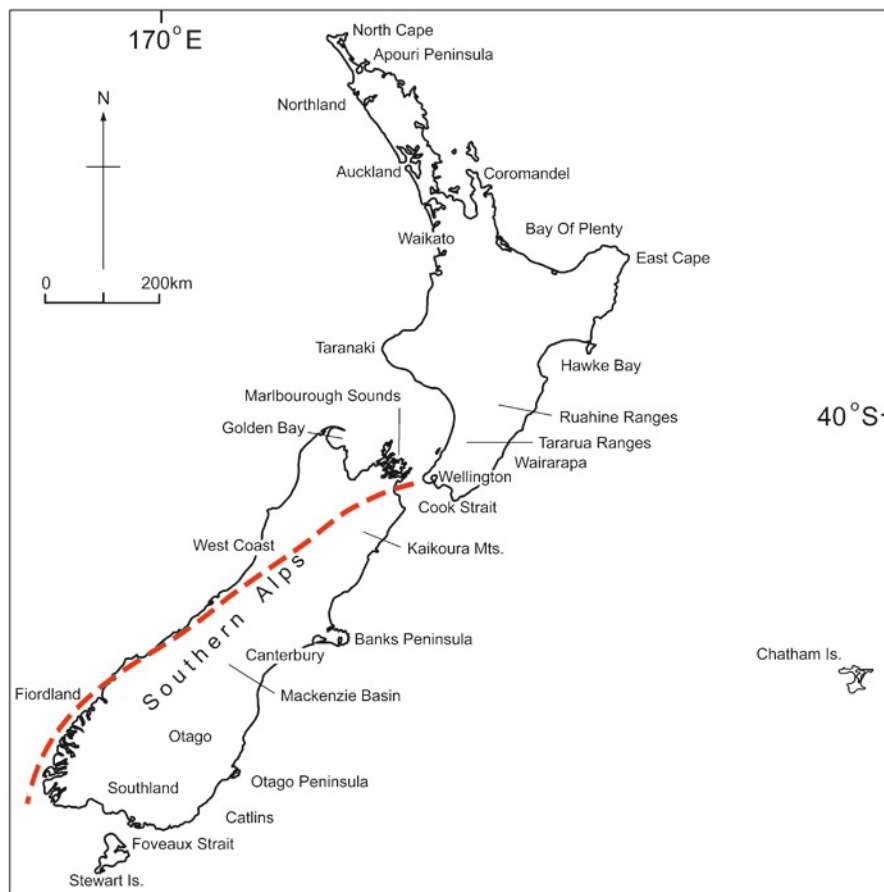


Fig. 2.1 The main islands of New Zealand, and larger nearby islands, mountain ranges and localities mentioned in the text; dotted red line represents the New Zealand Alpine Fault that lies along the boundary between the Australian and Pacific tectonic plates

perhaps resembles the Japanese archipelago, which is northern temperate at quite high latitudes with area c. 378,000 km². Japan is thus rather larger in area than New Zealand and has many more islands (>3,000). Or Great Britain, also northern temperate, has area c. 210,000 km². But New Zealand has been as geographically remote from other lands as it now is for perhaps 60 million years, whereas Japan and Great Britain, and also Borneo, have been much more intimately and recently connected to other major continental areas. So, New Zealand has a quite distinctive place in global geography, having long been greatly isolated from all other lands, both large and small, and both spatially and climatically. It was, of course, not always like that, as I discuss below, when I explore its ancestral connection to Gondwana.

2.2 The New Zealand Islands

The three larger islands of New Zealand form a slender, largely north/south-oriented archipelago, around 1,700 km long (Fig. 2.1), that spans about 13° of latitude (34–47°S). The three main islands are quite narrow, meaning that no locality is more than c. 200 km from the sea, and most places are, of course, much closer to the sea than that, even in the middle of the main islands. In addition, there are numerous associated small islands, with 250 of area greater than 8 ha. The larger ones to the north, include the Kermadec Islands (800–1,000 km northeast of mainland New Zealand and at c. 29–31.5°S) and Three Kings Islands (just 55 km north of northern New Zealand at c. 34°S), or substantially more southern, such as the Auckland Islands (at c. 51.5° and 465 km south of New Zealand's main islands) and Campbell (52.5°S and 700 km south) Islands. About 800 km to the east of central New Zealand are the Chatham Islands. All of these islands sit on a common area of the earth's crust, sometimes referred to as Zealandia, which is thrust upwards by enduring collision between the Australian and Pacific Tectonic Plates – in fact were it not for this collision, New Zealand and its associated islands would not emerge above the surface of the sea at all (Campbell and Hutching 2007). Moreover, there are some geologists who are arguing that it has not always been emergent, but that it may have sunk entirely beneath the sea at times (see below).

2.3 New Zealand Climate

Towards the north of mainland New Zealand's climate is warm temperate (annual average air temperature around 16°C), but in the south it is cold temperate (c. 10°C). The more small, northern, and more isolated, Kermadec Island are rather warmer, whereas the more southern Campbell and Auckland Islands are sub-Antarctic and distinctly colder. Being so narrow, New Zealand's climate is substantially oceanic, extremes of weather being ameliorated by proximity to vast expanses of cool to cold ocean. Weather is strongly influenced by systems arriving from across the ocean to the west (the Roaring Forties). Orographic rainfall is generated as the moist air off the ocean rises and crosses the mountains and this is especially true when mountain ranges are close to the west coast, as they are in much of the South Island. New Zealand is highly mountainous, especially in the South Island, where the Southern Alps reach elevations greater than 3,500 m with numerous mountain peaks >3,000 m, the mountains generally extending along the elongated axis of the islands, trending from south-west in the south to north-east in the north, across the main islands. About 75% of the landscape is above 200 m (Wallis and Treweek 2009:3,549). Rainfall is moderate to high, c. 600–1,600 mm per year over most of the landscape, though some mountainous locations exposed to the west have 7,000 mm of rain, a few as much as 12,000 mm, some even 16,000 mm (Griffiths and McSaveney 1983; Brenstrum 1998; Salinger et al. 2004; Alloway et al. 2007). Rainfall tends to be heavier in winter than in summer, though there are no marked

seasonal extremes and heavy rainfall can occur at any time of the year. There is no strict desert, though there are areas of limited rainfall (<300 mm per year), especially in the rain shadow to the east of the high elevation Southern Alps.

A consequence of the country's narrow shape, extensive latitudinal range, and high mountains, is that there tend to be many short, steep, east- or west-flowing rivers, especially on the West Coast of the South Island, where there are high elevations close to the coastline. Abundance of rivers tends to be accentuated by the fact that the islands and their high mountain ranges lie athwart the strong westerly winds of the cool to cold temperate Southern Hemisphere 'roaring forties', so that there may be very high rainfall, especially where the mountains are close to western coasts – as is true of much of the South Island, and especially in the far south.

With the often heavy rainfall, and the hard rocks that are abundant in many catchments combined with steep gradients, most rivers have abundant coarse gravel and cobble substrates (in part explaining the spectacular success of introduced salmonid fishes, taken there in the mid-late nineteenth century to provide recreational angling, though with increasingly-recognised, serious impacts on the indigenous fauna – McDowall 1968, 1990, 2003, 2006; Townsend 1996). Though gravels abound in the rivers in most areas, there are areas of softer sandstone (unmetamorphosed) 'papa' geology, especially in the eastern North Island, where gravel substrates are less available. This may have negative impacts on species richness and abundance in the fish communities – as it has also for the distribution and abundance of the introduced salmonids in New Zealand (McDowall 1990).

2.4 New Zealand's Rivers and Lakes

Because of New Zealand's high mountain ranges and high rainfall, there are numerous rivers. The largely north/south orientation of the mountains along the axis of New Zealand means that the rivers tend to be short and to flow east or west, and there are more than 300 significant estuaries around the long coastline (McLay 1976). The combination of high rainfall and steep topography means that rivers tend to be swift flowing and erosive forces are strong. Most rivers have hard rock, coarse gravel substrates, though there are areas of softer, unmetamorphosed sandstone geologic formations where the river substrates are variously bedrocks, silts, muds and coarse sands. The largest rivers are the Waikato (North Island), that is 425 km long and has mean flow of 310 cumecs and the Clutha (South Island), which is 322 km long and has mean flow of 560 cumecs. A distinctive feature of New Zealand's rivers is a series of large, unstable, multiply-braided rivers crossing the eastern plains of the South Island, the plains themselves formed by erosive forces in the mountain ranges of the hinterland to the plains. New Zealand has many lakes, most of them small (Irwin 1975; Lowe and Green 1987; 1992), the largest, Lake Taupo, is in the central North Island, with area >600 km². Some lakes are at low elevations, often coastal/brackish, tidal lakes formed by coastal drift of beach gravels. Many are at moderate to high elevations, those in the eastern flanks of the Southern Alps in the South Island being

derived from deep valleys scoured by glaciers in the Pleistocene. North Island lakes are more often a product of volcanism that has affected many areas over the past 50,000 years. Other North Island lakes are coastal dune lakes at low elevations in localities not far from the sea. All of New Zealand's lakes tend to be young, most of them less than 20,000 years old. A few are more than 20,000 years old (Lowe and Green 1987, 1992), but none is really ancient. Many of the lakes, of what ever origin, are deep, clear and oligotrophic. Some of the glacial lakes are turbid as a result of deriving their water from glaciers (see Mosley and Duncan 1992 and Harding et al. 2004, for a broad and comprehensive perspective on New Zealand's fresh waters and their ecosystems). The relative youth of most New Zealand lakes has significant implications for the biogeography of their fish faunas (discussed at length, below).

2.5 Human Colonisation

It is often said of New Zealand that it was the last significant land on earth to be colonised by humans – Polynesian Maori arrived around AD 1,300 (Davidson 1984; McGlone 2006). Caucasians from Europe first encountered New Zealand in the mid seventeenth century (by the Dutchman Abel Tasman), arrived repeatedly over the following centuries, and began to colonise in a substantial way in the mid nineteenth century. The relative recency of its human occupation means that New Zealand has a perhaps stronger record of a substantial fauna and flora, uninfluenced by humanity, than almost anywhere else on earth – even despite the very substantial impacts associated with human settlement over c. 700 years. A considerable amount of our knowledge of the fauna depends on subfossil remains (Worthy and Holdaway 2002). It is perhaps partly because of the relatively recent arrival of Polynesian humans (around 800 years ago), and more recently, Caucasians (<200 years ago), that this slender archipelago has a special place in global biogeography. And, indeed it does: I have elsewhere referred to its fauna and flora being a 'global microcosm' (McDowall 2008) – that what has happened there across geological time scales reflects, at a small scale, some important aspects of what happened much more widely around the world.

2.6 Biogeographical Significance: The Interest of Darwin, Wallace and Others

The biogeographical significance of New Zealand has long been recognised. New Zealand did not feature much in Darwin's writing; in fact he told of leaving after a couple of weeks in the Bay of Islands, in northern New Zealand, with no regrets, commenting rather bitterly, on departure on 30 December 1835 that "I believe we were all glad to leave New Zealand. It is not a pleasant place ... the greater part of the English are the very refuse of society. Neither is the country itself

very attractive”, he thought (Darwin 1896), though he only saw one small area of the country and his negative attitude derived primarily from his encounter with the developing, rather lawless, Caucasian colonial community in northern New Zealand. Few, today, would agree with him.

New Zealand featured much less than some other islands, such as the Galapagos Islands, or even the Falklands in Darwin’s account of the voyage of the *Beagle* (Darwin 1896). But he did, nevertheless, recognise that the area was biologically distinctive. He concluded that “before the commencement of the Glacial period, when the Antarctic lands, now covered with ice, supported a highly peculiar and isolated flora. I suspect that before this flora was exterminated by the Glacial epoch, a few forms were widely dispersed to various points of the Southern Hemisphere by occasional means of transport, and by the aid, as halting places, existing and now sunken islands, and perhaps at the commencement of the Glacial period, by icebergs” (Darwin 1859, – ex Darlington 1965:4). Darwin warned that New Zealand was being invaded by European biotic elements that were rapidly becoming established in New Zealand as a result of the burgeoning colonisation of New Zealand by Caucasian peoples in the mid nineteenth century (Darwin 1873:309). Thus it is implicit that he recognised that the evolutionary processes taking place on the isolated New Zealand landscape might have been distinctive and would have resulted in idiosyncratic impacts on indigenous biota by the exotic species becoming established there (and he would prove correct – King 1984; Worthy and Holdaway 2002; McDowall 2006).

Some of the major conservation impacts of human presence in New Zealand actually dated from before Caucasian colonisation, resulting rather from the introduction to New Zealand by Polynesian Maori people of the Pacific rat or kiore, *Rattus exulans*, the Polynesian breed of domestic dog, *Canis familiaris*, and also from Maori harvest of moa, the large indigenous ratite birds of the family Dinornithidae, which became extinct as early as the fourteenth century (Worthy and Holdaway 2002:546; Gibbs 2009). There were also probable consequential impacts from moa extinction on other macrofauna, such as the very large eagle for which the moas were a primary prey (Worthy and Holdaway 2002). However, there is no evidence of adverse impacts from Maori harvest on any of the indigenous freshwater fishes, despite these fishes forming a major dietary source for the Maori people around New Zealand (McDowall in press).

Darwin (1873:349) clearly found New Zealand intriguing, and observed that “Although New Zealand is here spoken of as an oceanic island, it is in some degree doubtful whether it should be so ranked; it is of large size, and is not separated from Australia by a profoundly deep sea; from its geological character and the direction of its mountain ranges, the Rev. W.B. Clarke has lately maintained that this island, as well as New Caledonia, should be considered an appurtenance of Australia.” Others biologists would soon follow Darwin, in expressing fascination with variously distinct aspects of the New Zealand fauna and flora. A little later than Darwin, biogeographer Alfred Wallace (1880) was also intrigued by what little he knew of New Zealand, and he too had difficulty deciding whether the New Zealand land mass was a small continent or a large island. He alluded to it (p. 442) as an “anomalous

island.” He (p. 443) found that its “...geological structure has a decidedly continental character...” despite it being “...surrounded by a moderately deep ocean...” and (p. 444) he suggested that “...the most probable ancient connections...were with tropical Australia and New Guinea, and perhaps, at a still more remote epoch, with the great Southern continent by means of intervening lands and islands...[which] will serve to explain many of the remarkable anomalies which these islands present.” In the end he decided that it was probably some of both island and continent, and this was an insightful view, that was later confirmed by geological studies. All he could state about the freshwater fishes was that “...we need only say here, that none belong to peculiar Australian types, but are related to those of temperate South America and of Asia”, and in this he was wrong. Clearly, he was unaware of much of the early literature, despite having read some of the work of early colonial New Zealand biologist Frederick W. Hutton (Wallace 1880:449).

Founding mid-nineteenth century botanist Joseph Hooker (1853) examined the floras of southern lands and concluded that “land communications between” the major southern land areas were needed to explain the apparent similarities of the floras for higher orders of plants, but he thought that spore-bearing plant forms could have been carried long distances around the Southern Ocean in the “violent and prevailing westerly winds” that thrash southern lands, especially at high southern latitudes. So he proposed a mixed model of derivation that we would today ascribe to both dispersal and vicariance, though he would not have been familiar with the term vicariance, which is of much later origin.

2.7 Early New Zealand Biogeographers

Noted late nineteenth century New Zealand naturalist and geologist, Frederick Hutton was an avid early follower of Charles Darwin (Hutton 1902) and brought an evolutionary perspective to the geographical relationships of the New Zealand fauna. Of New Zealand he wrote (Hutton 1873:227). “Although small in size it contains a fauna and flora so peculiar that several naturalists consider it a separate biological province apart from the rest of the world. Isolated from any large continental area longer probably than any other portion of the earth, it contains the remnant of a population of a continent that existed before the Mammalia had spread over the world....New Zealand therefore presents us with what we may call the elements of a continental fauna, or a continental fauna in its simplest state, and consequently in that state which is most advantageous for studying the mutual relationships of the animals composing it.” Hutton alluded to both Darwin and Wallace regarding New Zealand as an “oceanic island...that has never formed part of a continental area since its emergence from the sea”, though Hutton, himself, concluded that the “New Zealand fauna may be correctly called the remnants of a continental fauna, and that a close study of it will throw great light on many of the most important, but at the same time most obscure problems in zoology.” Coming as it did in the 1870s, in an intellectual environment with no perception of the former

existence of Gondwana, or the phenomena of plate tectonics and continental drift, Hutton's perspective is significantly prescient. He added (p. 250): "If we now review the evidence adduced, and select the more important points we find in the distribution of the Struthious birds [ratites], the frogs, fresh-water fishes, several shells...Centipedes and *Peripatus* among the annelids [sic], evidence of a former great extension of land in the Southern Hemisphere, for these cases cannot all be accounted for by drifting icebergs." Hutton would have known nothing explicit about Zealandia. But, he (p. 251) envisaged a "continental period, during which South America, New Zealand, Australia, and South Africa were all connected, although it is not necessary that all should have been connected at the same time, but New Zealand must have been isolated from all before the spread of the Mammals....Subsidence then followed, and the evidence points to a second continent stretching from New Zealand to Lord Howe Island and New Caledonia....Such are, I think, the deductions that can be fairly drawn from a study of our fauna. It remains now to examine the geological and palaeontological evidence and see whether it agrees with that derived from zoology..." Hutton was familiar with New Zealand geology, as it was known in the 1870s, and from his examination, found significant concordance between what he observed of the fauna and what he knew of geology. It would certainly be interesting to watch Hutton's face, were we able to describe to him modern knowledge of geology which though extraordinarily different from the patterns and processes known to Hutton, would nevertheless probably have provided him with an explanation of the origins and derivation of the New Zealand fauna and flora that were even more satisfying than his own.

And, so, throughout the early period of natural history studies in New Zealand there has been repeated recognition of the distinctive nature of its fauna and flora; it was well served by several, early, fine and insightful naturalists and geologists.

2.8 Biogeography of the Modern Era

Equally, in more modern times, one biogeographer after another has extolled the distinctiveness of the New Zealand biota, and this has been true of individuals expounding highly divergent perspectives on New Zealand. Part of this interest has been the common recognition that New Zealand shares many of its plants and animals with other lands around cool temperate latitudes of the Southern Hemisphere, and in particular the combination of that shared biota and New Zealand's great geographical isolation – many observers were noticing this and asking "How could this be?"

Versatile and noted New Zealand geologist/naturalist Charles Fleming provided the first substantial modern descriptions of the history of New Zealand and its biota in a series of reviews (Fleming 1949, 1962, 1975, 1979) that progressively analysed the history of the landscape and provided a synthesis of that geological history and the country's natural history. American biogeographer Philip Darlington (1965:102) observed that the "geologic, climatic and biotic history of New Zealand is known in much more detail than the history of any other southern cold-temperate land", and this can be attributed substantially to local naturalists' interest in the region's

history across more than a century of studies (made accessible substantially by the writing of Fleming, cited above). I think he was right. And though Darlington recognised the advanced state of knowledge of New Zealand, much of what he derived from this knowledge was wrong. But (Darlington 1965:66) he regarded New Zealand as a “special case”, one of the first of many to do so. Modern American ichthyologist Gareth Nelson (1975:494) stated that “With regard to general problems of biogeography, the biota of New Zealand has been perhaps the most important of any in the world. It has figured prominently in all discussions of austral biogeography, and all notable authorities have felt obliged to explain its history. Explain New Zealand [he thought] and the world falls into place around it.”

New Zealand botanist McGlone (1990:57) found New Zealand “to some extent like an alternative universe. If we want to know what the world might have been like if vertebrates had never conquered the land [he urged], study New Zealand”. And, forecasting 100 years ahead, McGlone (1990:60) thought that “One thing we can be sure of is that [biologists] will still be fascinated by the only truly unique thing New Zealand has to offer the world: its biota.” American ornithologist and evolutionary biologist Jared Diamond (1990:3) regarded New Zealand as one of the “most interesting oceanic islands” (along with Hawaii, New Caledonia and Madagascar), and he thought it “as close as you will get to the opportunity to study life on another planet: New Zealand being “by far the largest, remote oceanic island”. However, he found it “interesting...also as the world’s smallest continent”. Moreover, he considered that New Zealand started off with the most important and interesting biota of any island....” British conservation botanist David Bellamy et al. (1990), saw New Zealand as having had “a starring role in the evolution of the living world,” and Australian Tim Flannery (1994:55) regarded New Zealand as comprising “a completely different experiment in evolution” from the rest of the world. New Zealand entomologist George Gibbs (2006:7) thought that New Zealand’s “isolation promoted evolutionary pathways that were impossible anywhere else” and he argued that “Its biological inhabitants have captured the imagination of naturalists ever since Joseph Banks” who was naturalist aboard the Endeavour with James Cook, when they were in New Zealand in 1769. Most recently, Wallis and Trewick (2009:3,548) described New Zealand as a “conundrum to biologists, possessing as it does geophysical and biotic features characteristic of both an island and a continent.”

These various commentaries point to enduring and widespread agreement about the distinctive nature of New Zealand’s biota, and a fascination with its evolutionary and biogeographical histories. It is in the context of all these studies and attitudes that I explore the biogeography of New Zealand’s freshwater fish fauna.

2.9 The Question of ‘Absence’ and ‘Extinction’

Several twentieth century biogeographers, some of them eminent biologists such as Americans George Simpson (1940) and Philip Darlington (1957, 1965) have made much of the lack of certain taxonomic groups in New Zealand, especially a lack of mammals or snakes (as had Darwin, Wallace, Hutton and others in the nineteenth

century). They all interpreted such absences as indicative of a lack of suitable former land connections between New Zealand and places where such groups are known to have been long present. I think this logic is seriously deficient as it fails to take into consideration the prolonged and substantial climatic and tectonic turbulence of Zealandia, the formative New Zealand land mass, and the implications of such turbulence for the New Zealand biota through the Cenozoic, particularly the role of extinction, of which there has clearly been a great deal: see Lee et al. (2001), for instance, who discuss large scale changes in the flora over time, particularly the loss of the more tropical to warm temperate elements, or Worthy and Holdaway (2002), who discuss more recent major extinctions in the bird fauna. Interestingly, Wallace (1880:69) seems to have had some awareness of this, writing: “The notion that if such animals existed their remains would certainly be found, is a superstition which, notwithstanding the efforts of Lyell and Darwin, still largely prevails among naturalists; but until it is got rid of no true notions of the former distribution of life upon earth can be attained.”

There is no reason to think that changes in the New Zealand freshwater fish fauna have been fundamentally any different from what these various workers document in the various and highly diverse groups they have studied. A lack of snakes is mentioned by the Americans George Simpson and Philip Darlington, and the absence of this group should occasion no great surprise given the severity of Pleistocene cooling. Equally, the absence of all sorts of groups is inevitable given the certainty that most of New Zealand was submerged by sea in the Oligocene (Fleming 1979), and some geologists have suggested that perhaps all of it was submerged (Landis et al. 2008). Thus, emphasising New Zealand’s lack of groups such as snakes or mammals as significant indicators of the lack of land connections fails to take into consideration the almost certain extinction processes across geological time as well as a failure, so far, to discover fossils that indicate that groups not now present were at some former time present in New Zealand. Actual examples relate, for instance, to the relatively recent discovery of Mesozoic dinosaurs (Molnar and Wiffen 1994; Wiffen 1996; Cox and Wiffen 2002), or of a crocodile (Molnar and Pole 1997), and most of all that there was once some kind of small, presumably non-volant, mammal in New Zealand (Worthy et al. 2006), and yet the absence of all of these groups has been cited as indicating a lack of ancient New Zealand land connections. I suspect not. Moreover, presence of some groups in New Zealand needs to be interpreted with great care and they may not actually indicate that there was some early land connection.

An interesting example of how ignorance of extinction might distort our understanding applies to the relationships of New Zealand’s short-tailed bat, *Mystacina*, which was long interpreted as indicating ancient connections probably with a primitive South American bat (e.g. Hutton 1873). However, recent fossil discoveries in Australia have revealed a fossil close relative of the New Zealand species (Hand et al. 1998, 2007), and so the purported close, if ancient, connection of the New Zealand bats to South American bats is simply mistaken. There may be similar issues relating to New Zealand’s primitive *Leiopelma* frog, which is connected by some to an equally primitive frog genus, *Ascaphus*, in North America. Much is

made of the obscurities of the relationships of this frog, but in all probability so little is known of its relatives or relationships that its presence is unlikely to be usefully informative in much the same way. Just as the tuatara, *Sphenodon*, comprises a likely ancient lineage that has survived nowhere else but in New Zealand (though fossils show the group to have once been widespread), *Leiopelma* and its relatives may also be much the same, though no doubt frogs are a group less prone to being preserved in accessible fossils, and there is really no other likely group of frogs with informative relationships.

Lee et al. (2001) have explored the history of the New Zealand flora and have revealed a host of sub-tropical plants that are no longer known from New Zealand, such as eucalypts and casuarinas, and so the present New Zealand flora is really very different in many details from what was present during the mid Cenozoic. And, closer to the subject of the present book, the description of just two scale fragments (see Fig. 1.12) of what seems likely to have been a basal perciform fish from the Miocene of Central Otago (McDowall and Lee 2005) demonstrates the former presence of a group of fishes for which there was formerly no faint hint of a presence here. Taken together, the various, quite recent fossil findings point clearly to the fragility of arguments based on absence of land connections attributed to absences of key taxa. As Simpson (1940) put it, "...the discovery of a single fossil mammal tooth in Antarctica could at once settle some of the most disputed aspects of the problem" of the distribution of mammals in southern continents. In essence, then, absence of knowledge of various groups is not a good indicator of the lack of any former land connection that might have facilitated arrival of such groups, i.e. absence today or from the fossil record is not a good foundation for arguing for historic absence. Darlington (1965:106) relates that biogeographers find it difficult to credit a land bridge that would be crossed by birds on foot but not be other contemporaneous land vertebrates, and he then argues for a lack of evidence for either a massive rush of life when a new land connection is made, or for biotic evidence for the ending of an old land connection, but I think he, too, has seriously underestimated the potential for historical extinction to be driven by perturbation, especially in New Zealand with its very vigorous geological history. And so when Darlington (1965:64) argued that New Caledonia and New Zealand do not have the animals they should have if the supposed land connection really existed", he seriously failed to factor extinction into his perceptions. Should we, then, really be surprised that, for instance, there are no snakes in New Zealand, given the intensity of the Pleistocene cooling?

But then Darlington (1965:64) also thought that the explanation of northern relationships of some New Zealand plants and animals is that dispersals into the southern cold-temperate zone have been much more complex than has usually been realised, and he argued for much more parallel invasion, re-invasion, and extinction, including extinction in Australia of the ancestors of many New Zealand plants and animals, and that these complex processes have produced the complex geographic relationships of the New Zealand flora and fauna today. He was probably right, but he didn't recognise the extent of the extinctions in New Zealand, as well, which combine to tell a very different story about the origins, nature and relationships

of the New Zealand biota, based on a hugely detailed floristic history described by Lee et al. (2001). When it comes to dealing with island biotas like that of New Zealand he (Darlington 1965:139) suggested that the “irreconcilable *cannot cross salt water and cannot have land connections* school of biogeographers should be abandoned in favour of a *let us look at the whole situation and see what happens* school” (original italics), and there was a lot that he needed to learn, himself. It is a complex and imprecise matter.

One of the points that seem, to me, to need consideration is that when New Zealand and other Gondwanan lands were at much higher latitudes than they are now, one of the critical elements influencing life would have been much reduced day length in winter – the closer lands were to the South Pole, the shorter winter day length would have been, and the implications for life might have been substantial – a question largely unstudied that I think merits attention.

2.10 Origins of the Freshwater Fish Fauna: Marine Derivations or Ancient Land Connections

One of the key issues, the question of whether diadromous fishes have marine origins, arises frequently in discussions of the derivations of fish faunas, especially the faunas on small islands where the presence of ‘freshwater fish’ might be regarded as surprising or unlikely. New Zealand has been no different. Stokell (1950:3) discussed this question at some length in a review of the biogeography of galaxiids. He found that the “problem of Galaxiid distribution has engaged the attention of many zoologists, but [he thought that] none of the explanations that have been advanced is satisfactory. The popular hypothesis of derivation from marine congeners, which is usually put forward without either the presentation of supporting evidence or a consideration of the circumstances that tend to discredit it, introduces problems almost as great as the one it attempts to solve. No attempt has been made to explain the *independent* adoption of a freshwater habit in each of the several countries and the subsequent extinction of the ancestral form *in three oceans*. If marine Galaxiids had been so well established as to have extended through the area involved, it might be expected not only that they would have persisted till the present time, but that they would have exceeded their freshwater derivatives in number of species.” He concluded (p. 4) that “no marine group from which the Galaxiids may be conceived to have evolved is apparent, and that the closest relatives of the family are freshwater dwelling”. He mulled over the prospect of “past connections [between] all the countries in which Galaxiidae is represented” and found the difficulties “less formidable if the hypothesis of drifting continents advance by Du Toit is substituted for the usual conception of connection by way of Antarctica. Whatever form of connection is postulated, it is essential that it should have been maintained until Galaxiidae was

evolved”, though if it was to be of any value, it would need to have been present until *Gl. maculatus*, itself, had evolved.

Stokell was unaware that several additional galaxiids have a marine whitebait stage (McDowall 1990), being adamant that only one species “is known to enter the sea”. He struggled, too, with the event that species of Retropinnidae, which are widespread on mainland New Zealand, are not recorded from the Auckland and Campbell Islands, expecting that “the means of distribution for the occurrence of Retropinnidae in such widely separated countries as Australia and New Zealand would have been sufficient to extend the family to the Auckland Islands”, but he perhaps thought that the family may once have been present but was exterminated by habitat change on those islands. However, here again, we confront the issue of absence, for which the explanation may simply be the stochastic nature of dispersal processes, added to the problem of self recruitment to small oceanic islands and/or a lack of suitable habitat and the question of extinction. Seemingly *Galaxias* is able to ‘manage’ this problem.

Stokell (1953:48) returned to this question, admitting that he had “no satisfactory explanation to offer.” He stated that it was his “purpose in bringing the subject forward to point out the weaknesses of current hypotheses and present such evidence as [he] had been able to gather in the hope that some of its latent features may be brought out in discussion.” He explored all manner of possibilities, including, again, the prospect of multiple derivation from a marine ancestor and the existence of former land connections but then, unaware of the now recognised extent to which various *Galaxias* species go to sea, had no solution to offer.

American ichthyologist Carl Hubbs (1952:325) explored the question of bipolarity, where related groups are found at high latitudes in both the Northern and Southern Hemispheres (sometimes such groups are called bizonal, bitemperate or amphitropical), and he recognised that this is an issue for lampreys of the families Petromyzontidae (northern) and Geotriidae (southern) and also alluded to this for the “distinctive and primitive [southern] teleost families Galaxiidae, Aplochitonidae, Retropinnidae and Prototroctidae”, and though he did not specify their northern counterparts, Hubbs noted “Their trenchant separation from not clearly recognizable Holarctic representatives indicates prolonged isolation.” At that time, Galaxiidae were regarded as related to the northern cold temperate Esocidae whereas a relationship between the southern Retropinnidae and the northern Osmeridae was current (and is still held – McDowall 1969; Johnson and Patterson 1996; Waters et al. 2000). Both sets of families can appropriately be described as bipolar. In Hubbs opinion the southern families are “ancient, probably pre-Tertiary relicts of groups that have failed to persist in the Tropics, either because of unfavourable physical conditions or because they were unable to compete with the rich faunas that have evolved there”, but he provided no hint that any of these groups had ever populated tropical latitudes and it is dubious that they ever did. Thus, little is known about how the bipolarity of these two significant and primitive groups of fishes, and their present ranges at high latitudes in both Northern and Southern Hemispheres, was attained – a biogeographic question of some interest.

2.11 Darlington, Gondwana, Plate Tectonics and Continental Drift

American biogeographer Philip Darlington really struggled with developing an appropriate and coherent explanation for the distinctive fauna and flora of New Zealand. His 1965 book sat at the cusp of the emergence of plate tectonics and the acceptance of continental drift. He conceded (and I think that is a more appropriate word than 'concluded') (Darlington 1965:210) that "Evidence from several independent sources...has forced me to conclude that the southern continents have drifted. I have therefore become a Wegenerian, but not an extreme one. I doubt the former existence of a Pangaea or Gondwana, and I think that movements of the continents have been simpler and shorter than most Wegenerians suppose" ...so he had 'became a Wegenerian' without really becoming one, and this constrained his entire book. He was even uncertain that Africa and South America were ever closely joined and if they ever were, he seemed to have wanted this rather too early in geological history and without any significant implications for Antarctica. Thus, Darlington wrote his last biogeography book about 5 years too soon, or perhaps if had been a younger man he might have embraced continental drift more wholeheartedly. He seems to have accepted an almost "Clayton's" version which in the end was no useful version at all. I well recall being a post-graduate student in the Museum of Comparative Zoology, at Harvard, where Darlington worked, and we students were told that Darlington's book was available in the book shops, and we all rushed off to buy a copy. For us 'brash young students' it was somewhat a serious disappointment and, I think, a sad end to a distinguished career.

But Darlington (1965:65) was I think right in stating that biogeographers, including himself, "often greatly underestimate the multiplicity and complexity of plant and animal dispersal everywhere." About New Zealand, he concluded (Darlington 1965:214), that it "...has probably been isolated since the Carboniferous (or longer), has received its life across deep ocean barriers. And, because New Zealand has received a large proportion of the groups of terrestrial organisms characteristic of other far-southern lands...I think that these plants and animals crossed ocean gaps to New Zealand and that many other plants and invertebrates of the same general groups may have crossed water gaps elsewhere in the Southern Hemisphere." So, in the end, given modern discoveries, he was more correct than he knew, and more correct than he is sometimes given credit for (Brundin 1966), in view of the impetus given to the role of dispersal for the whole New Zealand biota as a result of the 'molecular revolution.' Many modern biogeographers, 40+ years later, would actually probably say much the same as Darlington, except that they would find that the physical isolation of New Zealand was much more recent in its history. They would, of course, have viewed global geological processes relating to the changing positions of lands very differently from Darlington, but much of this geological change is believed to have taken place prior to much of the now widely accepted dispersal that provided New Zealand's with its fauna and flora (see below).

2.12 So, What Is the Role of Dispersal?

Where distributions depend on dispersals, presence/absence of species is conditional on a species' capacity to disperse and the processes affecting dispersal, such as time and the availability of oceanographic and climatic influences; hence dispersal is driven in part by probabilities, as explored in detail by Simpson (1940, 1952). However, it does, of course, depend also on the availability of congenial habitats at the destination of the dispersal. Where these factors apply, absence has low biogeographic information value, and it tends to be meaningless or only marginally informative. I recall presenting a paper at a biogeographic conference discussing dispersal processes around the cold Southern Hemisphere in the galaxiid fishes, and was asked why, if fishes like *Galaxias maculatus* could have dispersed across the southern Pacific Ocean from New Zealand or Australia, to Patagonian South America, was this species also not present on Juan Fernandez, which lies partway across the Pacific and is at appropriate latitudes? My response was that I wasn't much interested in things that didn't happen. This was not intended to be simply dismissive, but to draw attention to the fact that dispersal is a highly contingent, and yet substantially random process. *Galaxias maculatus* may never have approached the shores of these tiny specks of island in the vast Pacific Ocean (they are a hugely smaller target than the west coast of Chile). But it also may have done so but have failed to colonise or survive there, or there may not be suitable habitats. Moreover, given that this species spends about 6 months as a small juvenile in the ocean (McDowall 1990), it is possible that, should it have ever arrived at Juan Fernandez, ongoing self-recruitment to that island might have been so difficult that maintenance of a population would be impossible. Given these points, it is interesting that the southern rock lobster, genus *Jasus*, is present on Juan Fernandez and must also face similar recruitment difficulties, and also that *Gl. maculatus* is present on Lord Howe Island, a similar tiny island in the Tasman Sea northwest of New Zealand, and it would be interesting to determine whether it recruits to Lord Howe on a regular basis, and whether this is based on self-recruitment or its recruitment derives from elsewhere, perhaps eastern Australia or New Zealand.

If New Zealand did become completely submerged at some time in the Cenozoic, as Landis et al. (2008) have hypothesised (see Chapter 3), there is a sense in which continental drift, plate tectonics, and Gondwana are almost irrelevant to terrestrial and freshwater biogeography. Under the scenario presented by Landis et al. everything that lives in New Zealand must have dispersed there after land again emerged from the sea. Even if New Zealand did not submerge entirely, so much of it probably did and so little of it remained emergent, that most of the biota has a post-submergence, dispersal origin anyway, and the relictual biotic elements that might have managed to survive through a clearly extensive but perhaps only partial submergence can, I think, be viewed as a few fascinating odds and ends that are substantially marginal to the evolution of the New Zealand biota over the last 20 million years (McDowall 2008) – a few elements that Gibbs (2006:202) described as “emblems” of former land connections, the “ghosts of Australis, living remnants

from the time when Antarctica was the focal point of the elongate continental block that spanned the South Pole and included Australia, New Zealand, New Caledonia and southern South America". If we did not have these "emblems", the biogeography of New Zealand would not really be substantially different. As Gibbs recognised, we are increasingly finding that fewer and fewer of the supposedly 'iconic' Gondwanan elements in the New Zealand biota are actually relicts of ancient, Gondwanan Zealandia. The present biota can be credited with far more dispersal than many biogeographers would have credited 30 years ago, even including *Nothofagus*, which Darlington described as the most characteristic element of the southern cool-temperate zone. Chapple et al. (2009:472) concluded that "Although some taxa appear to have Gondwanan origins, the majority of the biota has colonised New Zealand since it separated from Gondwana." Even *Nothofagus* is now believed to have dispersed around the Southern Ocean. Wallis and Trewick (2009:3,556) conclude that "two sub-genera of *Nothofagus* dispersed to New Zealand in the Oligocene, consistent with the absence of fossil pollen in New Zealand before this time." That does not mean that there was no association with Gondwana, but, rather, that the historical processes involved in *Nothofagus* achieving its contemporary distribution patterns have been far more complex and represent an ancient Gondwanan scenario overlain by the products of rather more recent, transoceanic dispersal processes. The same was almost certainly true of the entire biota, including the freshwater fishes (McDowall, 1978, 1990). The 'safety-net' of parsimony (the ostensibly most simple explanation) makes for misleading simplicity and is, in the end, unhelpful. Winkworth et al. (2005) reviewed the relationships of the New Zealand flora in considerable detail, and explored the origins of much of the alpine flora, in particular citing dispersal derivations from a surprisingly large number of sources, as far afield as temperate lands in the Northern Hemisphere and the South American Andes. They conclude a dispersal origin of the flora that is now well-embedded in contemporary understanding of its derivations. Equally interesting and surprising has been the role of New Zealand as a source of biotic elements for other lands, some of them far distant, including Hawaii. Wallis and Trewick (2009:3,548) very recently summarised that "It has become increasingly apparent that most of the biota of New Zealand has links with other southern lands (particularly Australia) that are much more recent than the breakup of Gondwana. A compilation of molecular phylogenetic analyses of c. 100 plant and animals groups reveals that only 10% of these are even plausibly of archaic origins, dating back to the vicariant splitting of Gondwana from Gondwana ... even lower." But, it seems clear that some ancient biotic elements may have such origins.

A great deal of passion that has surrounded this prolonged and mostly healthy debate about the role of Gondwana in the history of the New Zealand biota. Boyer and Giribet (2009:1,085) ask "is there a truly Gondwanan character to the New Zealand flora and fauna?" and they alluded to the question of a Gondwanan origin for the New Zealand biota being the subject of fierce debate over the past few years, with some [biogeographers] maintaining that Gondwanan vicariance has played a major role in establishing the biota of New Zealand...and others insisting that submergence of New Zealand during the Oligocene and/or long distance dispersal to the archipelago

have erased any Gondwanan signal in extant communities.” The depth and vigour in this debate can, perhaps, be gauged from the titles of some recent contributions to this debate: “Goodbye Gondwana” (McGlone 2005); “Ghosts of Gondwana” (Gibbs 2006); Goodbye Gondwana: New Zealand biogeography, geology and the problem of circularity” (Waters and Craw 2006); “Hello New Zealand” (Trewick et al. 2007); and “Welcome back New Zealand...” (Boyer and Giribet 2009). From time to time throughout this book, we will confront this very fundamental question, with comments from some geologists and biogeographers that New Zealand was completely submerged during the Oligocene, and lists of taxa that seem, to some, myself included, that might be indicators that there was always some land there for animals and plants to live on.

References

- Alloway BV, Lowe DJ, Barrek DJA, Newnham RM, Almond PC, Augustinas PC, Bertler NAN, Carter L, Litchfield NJ, McGlone MS, Shulmeister J, Vandergoes NJ, Williams PW (2007) Towards a climate event stratigraphy for New Zealand over the past 30,000 years (N Z-INTIATE project). *J Quatern Sci* 22:9–35
- Bellamy D, Springett B, Hayden P (1990) *Moa's ark: the voyage of New Zealand*. Viking, Auckland, N Z, 231 pp
- Boyer SL, Giribet G (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophalmi). *J Biogeogr* 36:1084–1099
- Brenstrum E (1998) *The New Zealand weather book*. Craig Potton, Nelson, N Z, 128 pp
- Brundin L (1966) Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptgyiae. *Kung Sven Vetenskap Hand* 11:1–472
- Campbell HJ, Hutching G (2007) *In search of ancient New Zealand*. Penguin, Auckland, N Z, 239 pp
- Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Mol Phyl Evol* 52:470–487
- Cox G, Wiffen J (2002) *Dinosaur New Zealand*. Harper Collins, Auckland, N Z, 39 pp
- Darlington PJ (1957) *Zoogeography: the geographical distribution of animals*. Wiley, New York, NY, 675 pp
- Darlington PJ (1965) *The biogeography of the southern end of the world*. Harvard University Press, Cambridge, MA, 236 pp
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for existence*. Murray, London, 502 pp
- Darwin C (1873) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for existence*, 6th edn. Murray, London, 458 pp
- Darwin C (1896) *Journal of researches into the natural history and geology of the countries visited during the voyage of HMS Beagle round the world*. Nelson, London, 615 pp
- Davidson J (1984) *The prehistory of New Zealand*. Longman Paul, Auckland, N Z, 270 pp
- Diamond JM (1990) New Zealand as an archipelago: an international perspective. *Conserv Sci Publ* 2:3–8
- Flannery TF (1994) *The future eaters: an ecological history of the Australasian lands and people*. Reed, Chatswood, NSW, 423 pp
- Fleming CA (1949) The geological history of New Zealand. *Tuatara* 2:72–90

- Fleming CA (1962) New Zealand biogeography: a palaeontologist's approach. *Tuatara* 10: 53–108
- Fleming CA (1975) The geological history of New Zealand and its biota. In: Kuschel G (ed) *Biogeography and ecology in New Zealand*. Monogr Ecol 27:1–86
- Fleming CA (1979) *Geological history of New Zealand and its life*. Auckland University Press, Auckland, N Z, 141 pp
- Gibbs GW (2006) *Ghosts of Gondwana. The history of life in New Zealand*. Craig Potton, Nelson, N Z, 232 pp
- Gibbs GW (2009) The end of an 80-million year experiment: a review of evidence describing the impact of introduced rodents on New Zealand's 'mammal-free' invertebrate fauna. *Biol Invas*. 11:1587–1593
- Griffiths GA, McSaveney MJ (1983) Hydrology of a basin with extreme rainfall: Cropp River, New Zealand. *N Z J Sci* 26:293–306
- Hand SJ, Murray D, Megiriam M, Archer M, Godthelp H (1998) Mystacinid bats (Microchiroptera) from the Australian tertiary. *J Paleontol* 72:538–545
- Hand SJ, Beck R, Worthy TH, Archer M, Sige B (2007) Australian and New Zealand bats: the origin, evolution and extinction of bat lineages in Australasia. *J Vert Paleontol* 27:86A
- Harding J, Mosley MP, Pearson C, Sorrell B (2004) *Freshwaters of New Zealand*. New Zealand Hydrological Society/New Zealand Freshwater Sciences Society, Christchurch, N Z
- Hooker JD (1853) Introductory essay to the flora of New Zealand. Lovell Reeve, London, 34 pp
- Hubbs CL (1952) Antitropical distribution of fishes and other organisms. *Proc 7th Pac Sci Congr* 3:324–329
- Hutton FW (1873) On the geographical relations of the New Zealand fauna. *Trans Proc N Z Inst* 5:227–256
- Hutton FW (1902) *The lesson of evolution*. Duckworth, London, 101 pp
- Irwin J (1975) Checklist of New Zealand lakes. *N Z Oceanog Inst Mem* 74:1–160
- Johnson GD, Patterson C (1996) Relationships of the lower euteleostean fishes. In: Stiassny ML, Parenti L, Johnston GD (eds) *Interrelationships of fishes*. Academic, New York, pp 251–332
- King CM (1984) *Immigrant killers*. Oxford University Press, London, 224 pp
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to paleogeography and climate. *Aust J Bot* 49:341–356
- Lowe DJ, Green JD (1987) Origin and development of the lakes. In: Viner A (ed) *Inland waters of New Zealand*. *N Z Dep Sci Indust Res Bull* 241:1–64
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 107–143
- McDowall RM (1968) Interactions of the native and alien faunas of New Zealand and the problem of fish introductions. *Trans Am Fish Soc* 97:1–11
- McDowall RM (1969) Relationships of the galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:93–108
- McDowall RM (1990) *New Zealand freshwater fishes: a natural history and guide*. Heinemann-Reed, Auckland, N Z, 553 pp
- McDowall RM (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Trans Am Fish Soc* 132:229–238
- McDowall RM (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool temperate galaxioid fishes. *Rev Fish Biol Fisher* 16:233–422
- McDowall RM (2008) Process and pattern in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM (in press) *Ikawai: freshwater fishes in Maori culture and economy*. Canterbury University Press, Christchurch, N Z

- McDowall RM, Lee DE (2005) Possible perciform scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *J R Soc N Z* 34:338–344
- McLay CL (1976) An inventory of the status and origin of New Zealand estuarine systems. *Proc N Z Ecol Soc* 23:8–26
- McGlone MS (1990) Global climate change and ecological complexity. In: Global climate change: proceedings of the Royal Society of New Zealand conference 14–15 June, 1990. Royal Society of New Zealand, Wellington, N Z, pp 56–62
- McGlone MS (2005) Goodbye gondwana. *J Biogeogr* 32:739–749
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of the biota. *Ecol Stud* 186:17–32
- Molnar RE, Pole M (1997) A Miocene crocodilian from New Zealand. *Alcheringa* 21:65–70
- Molnar RE, Wiffen J (1994) Polar dinosaur faunas from New Zealand. *Cretac Res* 15:698–706
- Mosley MP, Duncan MJ (1992) Rivers. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 91–106
- Nelson GJ (1975) Reviews: biogeography: the vicariance paradigm and continental drift. *Syst Zool* 24:490–504
- Salinger J, Gray W, Mullan B, Wratt D (2004) Atmospheric circulation and precipitation. In: Harding J, Mosley P, Pearson C, Sorrell B (eds) *Freshwaters of New Zealand*. Hydrological Society of New Zealand/New Zealand Limnological Society, Christchurch, N Z, pp 2.1–2.18
- Simpson GG (1940) Antarctica as a faunal migration route. *Proc 6th Pac Sci Congr* 2:755–768
- Simpson GG (1952) The probabilities of dispersal in geological time. *Bull Am Mus Nat Hist* 99:163–176
- Stokell G (1950) Freshwater fishes from the Auckland and Campbell Islands. *Cape Expedition Ser Bull, N Z Dep Sci Indust Res* 9:1–8
- Stokell G (1953) The distribution of the family Galaxiidae. *Proc 7th Pac Sci Congr* 4:48–52
- Townsend CR (1996) Invasion biology and ecological impacts of brown trout, *Salmo trutta* in New Zealand. *Biol Conserv* 78:13–22
- Treweek SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Wallace AR (1880) *Island life: or the phenomena and cases of insular faunas and floras, including a revision and attempted solution of the problem of geographical climates*. McMillan, London, 526 pp
- Wallis GP, Treweek SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Waters JM, Craw D (2006) Goodbye Gondwana: New Zealand biogeography, geology and the problem of circularity. *Syst Biol* 55:351–356
- Waters JM, Lopez JA, Wallis GP (2000) Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthys: Galaxiidae): dispersal, vicariance and the position of *Lepidogalaxias salamandroides*. *Syst Biol* 49:777–795
- Wiffen J (1996) Dinosaurian palaeobiology: a New Zealand perspective. *Mem Queensl Mus* 39:725–731
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Divers Evol* 8:237–247
- Worthy TH, Holdaway RN (2002) *The lost world of the moa: prehistoric life in New Zealand*. Canterbury University Press, Christchurch, N Z, 718 pp
- Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD (2006) Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, south-west Pacific. *Proc Nat Acad Sci USA* 103:19419–19423

Chapter 3

New Zealand's Geological and Climatic History and Its Biogeographical Context

Abstract New Zealand is part of Zealandia, an ancient continent that originated along the margins of East Antarctica in the late Cretaceous, and formed along the joint edges of the Australian and Pacific tectonic plates. It has been as isolated in the southwestern Pacific Ocean as it is today, for about 60 million years. The Chatham Islands are young and volcanic, having been emergent only for a few million years, and the Auckland and Campbell Islands to the south for a little longer, none of these islands having had land connections to the main islands since they emerged from the sea. Despite its Gondwanan origins New Zealand's biogeography probably has few direct biotic connections to these origins because most, perhaps all, of its present land surface was submerged by Ocean in the Oligocene. It is widely believed that most of its biota has dispersal origins, mostly from Australia, but also far more widely. New Zealand was warm temperate with low relief in the Miocene, but climatic cooling since then, linked also with substantial mountain building has led to the evolution of a distinctive alpine biota.

Keywords Cenozoic • Climate change • Dispersal • Geology • Glaciation • Gondwana • Mountain building • Plate tectonics • Volcanism

3.1 Background

Any regional biogeography must be viewed against a background of the subject area's geological and climatic history. It can probably reasonably be assumed that the most recent, significant, geological events will have left the greatest biogeographical imprint (McGlone 1985; Gibbs 2006; Campbell and Hutching 2007; McDowall 2008), though there are bound to be some emergent, residual effects of earlier events that remain 'visible' through the more recent impacts. Identifying the biogeographical imprints and impacts of these earlier events will likely be much harder than for more recent ones, partly just because of the passage of time, and partly because the effects of more recent events overlie, obliterate, or "overwrite" the impacts of earlier ones (Waters and Craw 2006).

Though New Zealand presently comprises a long slender archipelago of three main islands situated in the cool to cold temperate southwestern Pacific Ocean (see Fig. 1.1), its internal and external land connections, physical shape, latitudinal position, and climate, have all varied widely through the area's geological past. Thus, local temporal variation in climate is likely to be a complex amalgam of:

1. Global climate change
2. The shifting latitudinal position of the New Zealand landmass across time/history
3. Changes in the elevations of areas within that landmass owing to mountain building and erosion

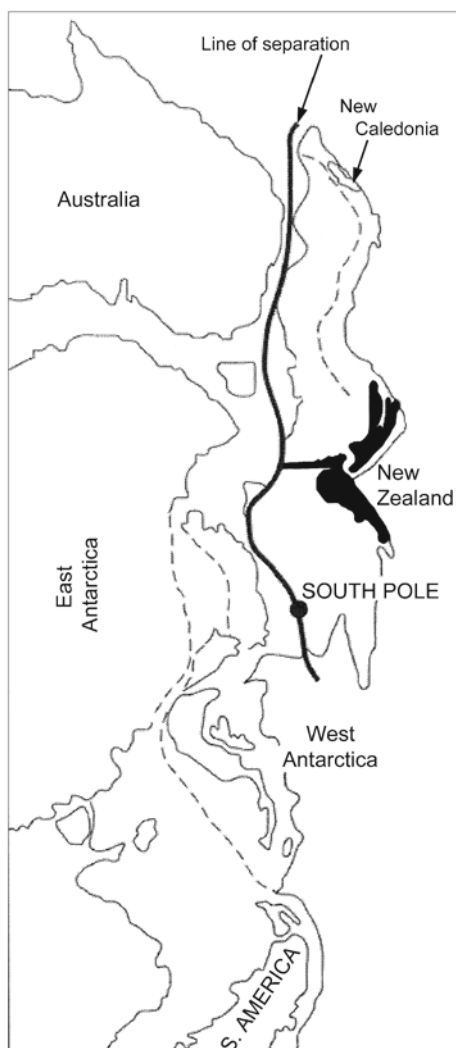
3.2 New Zealand's Origins

As an identifiable geological entity, New Zealand's history began along the shores of eastern Gondwana, close to Australia, and between it to the west and South America to the east (Fig. 3.1). Hints of this ancient Gondwanan connection are perhaps evident from the presence of some quite diverse known, Cretaceous dinosaurs (Molnar and Wiffen 1994; Wiffen 1996; Holdaway and Worthy 2006). A crocodile (Molnar and Pole 1997) and a likely mammal (Worthy et al. 2006), both of Miocene age, may also have been present on primordial New Zealand as it became detached from Gondwana. This landmass really includes a much more extensive area than modern New Zealand, and comprises a small continent that extends from present-day New Caledonia in the north, the present-day Lord Howe Rise and the Norfolk Ridge, south and east as far as the Chatham Islands, and south to the Campbell Plateau. Sometimes known as Zealandia (or primordial New Zealand; Campbell and Hutching 2007; Adams et al. 2008), this mini-continent became detached and moved away quite rapidly from the rest of Gondwana very early, beginning probably in the late Cretaceous, more than 80 million years ago (Cooper and Millener 1993; McLoughlin 2001; Campbell and Hutching 2007). At this time there were mountains in Zealandia that had been produced during the Rangitata orogeny, though these had become eroded to produce a peneplain of low relief by the end of the Cretaceous (Fleming 1979; McGlone 1985), so that there were no significant mountain ranges at that time. Geologists tell us that Zealandia moved quickly away from Gondwana, and thus from primordial Australia – which itself became separated from Gondwana much later. The early displacement of New Zealand established strong oceanic separation between it and Australia, roughly equivalent to the present distance (c. 2,000 km), by as early as 60 million years ago.

3.3 Development of the New Zealand Landscape

Kamp (1992) regarded the fact that the New Zealand land-mass lies along an active fault boundary (between the Australian and Pacific plates) as a fundamental driver of its landform development. Now-emergent land areas are only a small fraction of

Fig. 3.1 New Zealand's ancestral position, as a part of Zealandia, attached along the shores of Gondwana during Cretaceous times, before shifting off into the ancestral southern Ocean



the total Zealandia subcontinent; however, most earth materials comprising the present, emergent New Zealand landscape have a marine heritage (Waters and Craw 2006; Campbell and Hutching 2007; Craw et al. 2008; Landis et al. 2008), and there is little or no evidence for ancient, temporally-continuous, emergent land surfaces. At an early stage the New Zealand 'continent' almost certainly included land connections between the present main islands (though in very different shape and topography), and possibly also with the more remote Chathams, about 800 km to the east. During the Oligocene, Zealandia is described as being stretched and thinned, and this thinned earth crust became extensively submerged by a marine transgression (Trewick et al. 2007; Landis et al. 2008; Neall and Trewick 2008; Chapple et al. 2009; Wallis and Trewick 2009), and well over 90% of it is still submerged.

Whether the Chathams were always emergent above sea level is another question presently being investigated and debated (Campbell et al. 1993; Campbell and Trewick 2003). Campbell and Hutching (2007) are adamant that the contemporary, emergent Chatham Islands are relatively recent, perhaps only 2 million years old. Campbell Island, and perhaps the Aucklands and Antipodes, both well to the south-east, are said to have arisen during the Miocene from volcanism, were initially submarine, and are believed to have never been linked to the main islands of New Zealand (but see Michaux and Leschen 2005, for another perspective); the Three Kings Islands, just 55 km to the north of northern New Zealand, are thought to be of Pliocene age, and are also considered to have never been connected to the mainland (Fleming 1979). And the Kermadec Islands, 800–1,000 km to the north-east include active volcanoes and are also probably of similar age. Much further to the north again is New Caledonia which Hill (1996) considered may have had “floral interchanges with Queensland and New Zealand until the end of the Palaeocene”, and so perhaps until 30–40 million years ago (McLoughlin 2001; Sanmartin and Ronquist 2004; Gibbs 2006; Campbell and Hutching 2007). Today, no more than 10% of the surface of Zealandia is emergent (Mortimer 2004).

Much the largest of any postulated residual Oligocene islands (Fleming 1979) corresponds to part of the present southern/south-eastern South Island and Stewart Island (Fig. 3.2, arrow 3). Possibly, additional emergent areas at that time included northwest Nelson (arrow 2) and, in the north, what are now the Coromandel Peninsula and another small area in the vicinity of Raglan/Kawhia (arrow 1). Emergent land area certainly increased greatly during the later Oligocene and Miocene, when New Zealand became a land of low relief with a warm to sub-tropical climate (Stevens 1980; McGlone 1985; Lee et al. 2001). Elevated temperatures in the Miocene, possibly by 8°C (Jones et al. 2009) were enough to equate to a northwards (equatorial) displacement of around 15° of latitude (Fleming 1979); thus temperatures in southern New Zealand would then have been, warm-temperate, and quite similar to those in northern New Zealand today. Whether or not some earlier Central Otago landscapes are residual from primeval Zealandia (Fig. 3.2, arrow 3), there is general agreement that by Miocene times the Central Otago land surface with low relief, had “a poorly integrated series of rivers and lake basins [that] ... merged into a single lake [that] may have covered most of central Otago” (McSaveney and Stirling 1992), an area of around 5,600 km² (Douglas 1986).

Moving on into the Pliocene (ca. 5 mya) several important processes profoundly affected the New Zealand landscape and climate. There was the likely inception, or at least a major acceleration, of uplift of New Zealand's mountain ranges owing to forces involved in convergent movements of the Australian and Pacific tectonic plates. This possibly began as long as 6–8 million years ago (Whitehouse and Pearce 1992; Newnham et al. 1999; Campbell and Hutching 2007), and it certainly accelerated around 5 million years ago, most of it probably taking place in the last 2 million years and it is still continuing (Craw et al. 1999, 2008). Total uplift may have been as much as 20,000 m (Whitehouse and Pearce 1992), though this was substantially counteracted by massive surface erosion. Nevertheless, there were

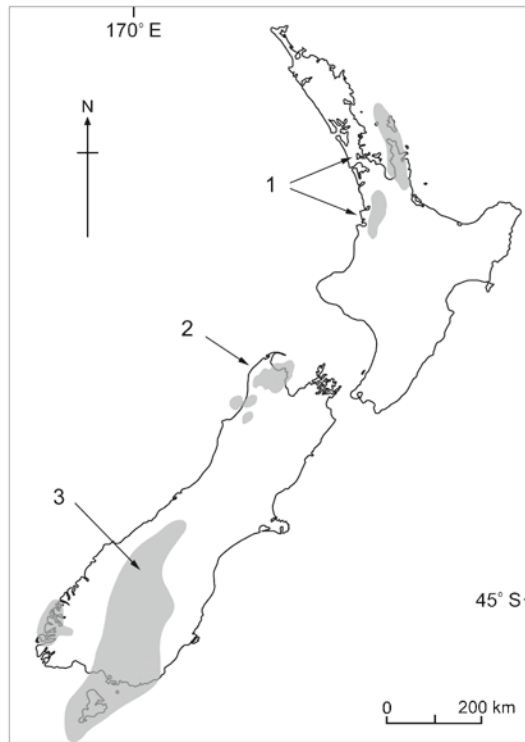


Fig. 3.2 Residual hypothetical emergent New Zealand islands during the Oligocene, a time of major marine incursion (after Fleming, 1979). **Arrows** – ↑1: two smallish islands in northern areas; ↑2: a small island in the Nelson area; ↑3: a major southern island related to the Otago Peneplain, perhaps extending north to the vicinity of the present Mackenzie Basin (some commentators think that Zealandia disappeared entirely beneath seas for a period, though this is controversial)

mountains over 3,000 m high in the Pleistocene (Chapple et al. 2009). One of the results of this erosion was the formation of the modern, broad, Canterbury Plains of the eastern/central South Island, although notably, there are not similar plains to the west of the Southern Alps. In addition to mountain uplift – when the “rising mountains first intersected the theoretical timber-line” (Fleming 1979), the late Pliocene and Pleistocene were times of widespread climatic cooling, so that the uplift of mountains and climatic cooling had additive effects on local climates in many areas, creating sub-alpine to alpine conditions for the first time in New Zealand since the Cretaceous. In the early Pliocene there was also extensive marine transgression across what is now the southern North Island (Fig. 3.3, arrow 1), and the southern coast of the North Island was across the present central North Island volcanic plateau. During this time, the northern South Island projected across the present Cook Strait to the southern North Island as the Whanganui-Marlborough shield (Fig. 3.3, arrow 2). Thus the northern half of the North Island had no land connection to other parts of the southern North Island.

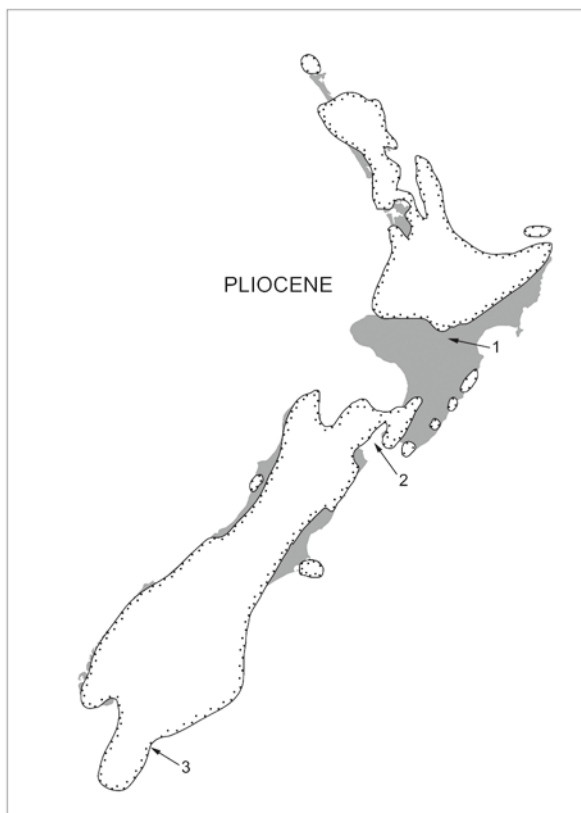


Fig. 3.3 New Zealand in the early Pliocene, with a small far northern island, the southern North Island submerged by sea and a peninsula of land connecting the northern South Island to what eventually became the southern North Island: **Arrows** – ↑1: submergence of the southern North Island – the so-called Manawatu Strait; ↑2: a land connection across the present Cook Strait to the southern North Island; ↑3: a land connection across the present Foveaux Strait between the South Island and Stewart Island

The broad sea-strait across the southern margins of a much reduced North Island was a substantial biogeographic barrier and there are biotic elements with southern boundaries that reflect that submergence. There was later uplift of the southern North Island, initially to form a low peneplain, across which the Manawatu River flowed westwards, and that river maintained a channel (the Manawatu Gorge) between what are now the Ruahine and Tararua Ranges, cutting down into the rock as the ranges rose (Lewis and Carter 1994), probably over the past 500,000 years (Whitehouse and Pearce 1992). Formation of a seaway through central New Zealand, analogous to the modern Cook Strait, probably formed first around 450,000 years ago (Lewis et al. 1994; Lewis and Carter 1994).

3.4 Glaciation

New Zealand underwent repeated, perhaps 20, cycles of major climatic change, cooling and warming (Lee and Forsyth 2008), beginning in the late Pliocene and continuing throughout the Pleistocene. These cycles, starting around 2.5 million years ago, resulted in extensive and repeated glaciations. Up to four cold major glacial episodes are recognised (Fleming 1979). The last, ‘Otiran’ glacial period began around 100,000 years ago, and lasted until c. 10,000 years ago, had at least three warmer interstadial periods, with its last major cold cycle around 25–15,000 years ago (Fleming 1979; McGlone 1985; McGlone et al. 2001). Wallis and Trewick (2009) estimated that 30% of the present South Island was then covered by glacial ice and snow. At the last glaciation the snowline was lowered by 850–1,000 m (Willett 1950; Wardle 1988). Contemporary New Zealand is presently in a warm interstadial period.

During periods of climatic cooling and glacial advance some areas were covered with seasonally-permanent ice sheets, especially in the western South Island (Fig. 3.4). Ice-sheets in the Southern Alps advanced westwards at times beyond present shorelines (Suggate et al. 1978; Fleming 1979), especially along the West Coast of the South Island, south of the small town of Ross (Fig. 3.4, arrow 3) (Soons 1992). Ice sheets descended further to the west of the mountain ranges than to the east owing partly to the source of precipitation being largely from the west to north-west, off the Southern Ocean. The steeper western (than eastern) slopes of the landscape may also have been influential. Further north in the western South Island there remained an ice-free coastal fringe, and some of the lowlands were also ice free (Fig. 3.4, arrow 2) (McGlone 1985; Soons 1992). The whole landscape into which the glaciers moved was not, however, believed to have been entirely ice covered. Especially in South Westland, where the gradients of the glaciers were very steep, some “interfluves” probably remained above the ice, with remnant pockets of vegetation that may have remained available to hasten plant recolonisation of the land surfaces that were present once the ice retreated (McGlone 1985; Soons 1992). Further to the south, Stewart Island, though reaching elevations of nearly 1,000 m, is not thought to have been as severely glaciated as the western South Island.

Eastern slopes of the South Island are somewhat in the rain-shadow of the South Island’s high mountain ranges (Fleming 1979; McGlone 1985), and as a result there was little glaciation on the eastern-central Otago Peneplain and south into Southland (Fitzharris et al. 1992; Craw and Norris 2003). Despite this, temperatures would have been cold (even more so than at present and the uplands of inland Otago are cold in winter, now). However aquatic habitats, unless completely frozen, would have never been colder than 0°C and the functionally important aspect of cold temperatures for freshwater animals may well have been the seasonal duration of the lowest temperatures, as much as the low temperatures themselves. Glaciers sometimes filled the big eastern intermontane valleys of the Southern Alps, spilling out beyond them onto the forming Canterbury Plains (Willett 1950; Soons 1979). Gage (1958), for example described how at the ‘Avoca’ glacial advance in the Waimakariri

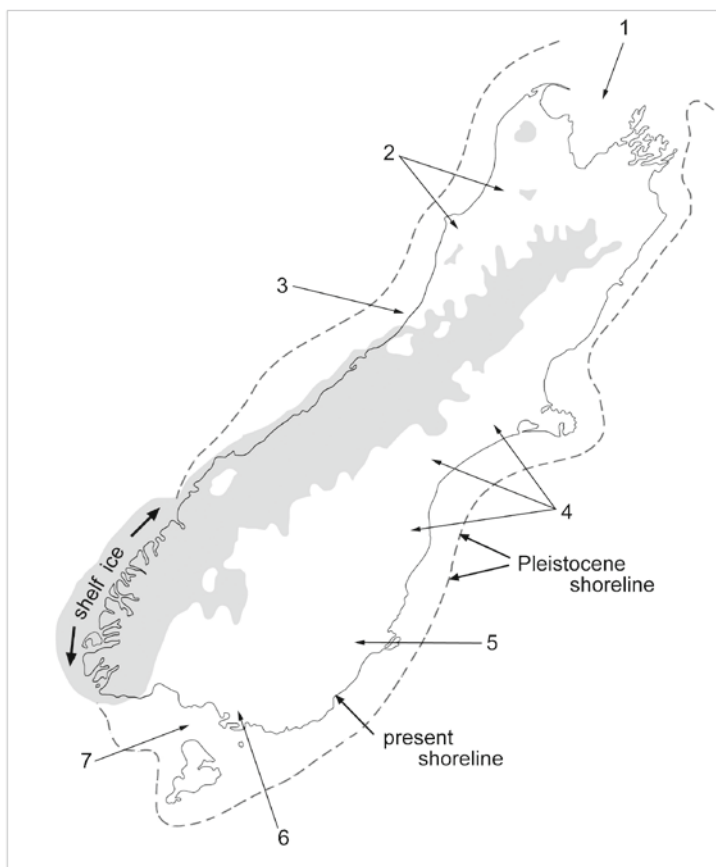


Fig. 3.4 The South Island at the time of peak the last (Otiran) Pleistocene glaciation (after Fleming, 1979). **Arrows** – ↑1: there was a land connection across Cook Strait to the southern sector of the North Island; ↑2: an area of the northern West Coast that was less intensely glaciated; ↑3: vicinity of town of Ross; ↑4: Canterbury Plains; ↑5: Otago Peneplain; ↑6: Southland Plains; ↑7: a land connection across what is now Foveaux Strait

River catchment, “ice overrode the lower flanks” of the eastern foothills of the Southern Alps. Glacial and interglacial periods of the Pleistocene were times of massive erosion of the glacial moraines, resulting in formation of the extensive, low-relief, Canterbury Plains to the east of the Southern Alps.

Glacial activity in the Southern Alps caused “overdigging” of troughs to depths appreciably below the general levels of the valley floors, sometimes even below present sea levels (Lee and Forsyth 2008) creating landforms suited to formation of glacial lakes, once the ice retreated, leaving glacial moraines that dammed the valleys (Soons 1992). This can be seen in numerous eastern South Island valleys, a significant number of which are now occupied by substantial, inter- or sub-montane, post-glacial lakes. These tend to be best recognised in the northern and eastern

slopes of the intermontane valleys of the Southern Alps (Lakes Rotoiti, Rotoroa, Sumner, Coleridge, Heron, Tekapo, Pukaki, Ohau, Wanaka, Hawea, Wakatipu, Te Anau, Manapouri), but there are also some along the western slopes of the Alps (glacial lakes like Mapourika, Wahapo, Paringa, Moeraki, and McKerrow). The imprint of the last (Otiran) glaciation was probably so strong that it obliterated much of the effect of earlier glacial episodes (Pillans et al. 1992).

The impacts of glaciation, per se, in the North Island at this time are thought to have been minor (Whitehouse and Pearce 1992), but the climate would have been substantially cooler than now, with the attendant biotic implications. No North Island glacial lakes are recognised, and permanent ice sheets and glaciers were minimal.

The glacial and interglacial periods saw several features of New Zealand geology and topography oscillating, in addition to climatic change. During the Pleistocene, Cook Strait, roughly as now known, was formed, though there were also times during that period when sea levels were lowered (as much as 130 m – Kirk 1994), resulting in land connections from the South Island to the southern North Islands, bridging the strait (Fig. 3.4, arrow 1). Lewis and Carter (1994) thought that before the end of the Miocene, the palaeo-geography and palaeo-oceanography of what became the Cook Strait region were “so different that analogy [homology?] with modern Cook Strait is probably inappropriate”. During periods of lowered sea levels at the glacial maxima, the shape of the land area was substantially altered, and this also established land connections between the southern South Island and Stewart Island (Fig. 3.4, arrow 7). As well, many of the small nearshore islands around the New Zealand coastline (such as Great and Little Barrier, and Kapiti Islands) became connected to the main islands (Fleming 1979; Lewis and Carter 1994; Lewis et al. 1994). The lowered sea levels would also have provided opportunities for new riverine connections to be made among adjacent river systems, which may have anastomosed across floodplains that extended up to 50 km or more beyond the present shores of New Zealand (Kirk 1994) (Fig. 3.4). These almost certainly sometimes included fluvial connections between North and South Island rivers now separated by Cook Strait, and the same was probably true of Foveaux Strait, with fluvial connections between the rivers of the southern South Island and Stewart Island (Fleming 1979).

At interglacial times when climate was warmer, the glaciers retreated and sea levels were higher, so that shorelines retreated inland, isolating some formerly confluent river catchments. A broad marine strait separated Aupouri Island (now equivalent to the present hilly area near North Cape – see Fig. 3.3) from Northland to the south, but the island became connected by formation of a sand tombolo during the Pleistocene (Fleming 1979; Brook 1999). Existence of several additional islands around southern New Zealand was also suggested by Fleming, which may have influenced the evolutionary and biogeographical history of New Zealand’s terrestrial biota, but these islands may have been too small and their streams too ephemeral to develop distinctive freshwater fish faunas. Certainly, there is nothing that suggests they had a still discernible role in that fish fauna’s history, as is true of the existing islands.

Craw et al. (2008) discussed processes that were associated with the uplift of the mountain ranges, especially the Southern Alps, and described events leading to headwater river captures along the mountain ranges, where relatively low passes formed and largely eastern mountain rivers were captured by rapid headwater erosion from the west driven by heavy rainfall. As a result the headwaters of several formerly eastern-flowing rivers were captured and diverted to the west. These processes must have had important implications for contemporary fish faunas, though the extent to which these implications persist to the present is a matter for detailed exploration.

It is likely that the major gravel erosion from the eastern Southern Alps that eventually formed the Canterbury Plains further to their east, took place from material that had been transported to the lower fringes of the mountain valleys during the glacial advances, was left there at times of glacial retreat, and then carried down the formative plains by the rivers draining the intermontane valleys. The huge alluvial fans that formed would have coalesced laterally, and the formative plains established a land connection between mainland South Island land areas (Canterbury) and Banks Peninsula (Kirk 1994), which had hitherto, at times, been a volcanic island (see Fig. 2.1; as James Cook mistakenly thought it was in eighteenth century). There was similar erosion of the Ruahine and Taranaki Ranges in the southern North Island that created gravel plains, such as in the Rangitikei-Manawatu area and the Wairarapa, where “alluvial aprons spread out from the rising ranges and the central volcanic zone of the North Island”, this also contributing to the bridging of North Island landscape to the south (Fleming 1979).

3.5 Volcanism

New Zealand has long had high levels of volcanism and, given that the islands lie along the junction of two huge tectonic plates, the Australian and Pacific, lively volcanism is unsurprising. There was major volcanic activity widely across Otago, in the mid-Miocene, c. 13–10 mya (Reay 2003). There was also some Pliocene volcanism in other areas such as at Mt. Pirongia in the Waikato in the central/western North Island, and in Banks Peninsula, and Otago Peninsula in the eastern South Island (Craw and Norris 2003), and later in the Pleistocene, in Coromandel in the northeastern North Island (Selby and Lowe 1992). Extensive volcanism took place over a wide area of the landscape during and since the Pleistocene. It seems likely, in a biogeographical sense, that the volcanism most influential in terms of terrestrial biota was also the most recent (McGlone 1985; McDowall 1996). Holocene volcanism was present in the Bay of Islands, the Auckland Isthmus, Taranaki and Taupo. The activity around Auckland dates back to around 160,000 years, but it persisted locally to very recent times – eruptions at Rangitoto Island, near Auckland, took place at least four times in the past 1,200 years, and most recently perhaps 225 years ago. Ballance and Williams (1992) identified at least 60 centres of historical volcanic activity around Auckland. In the western North Island Mt. Taranaki (see

Fig. 2.1), though now seemingly dormant, was another area of relatively recent major activity. As many as 76 eruptive events are recorded for Mt. Taranaki and nearby centres since 28,000 years ago, or once approximately every 330 years (Alloway et al. 1995); the last Mount Taranaki eruption was less than 300 years ago (Neall 1992), and so the volcano is scarcely ‘dormant’, even when viewed in human-history time scales. Lees and Neall (1993) suggested that restoration of vegetation, after an eruption event nearly 2,000 years before, may have taken c. 1,400 years.

Volcanism in the central, northeastern North Island has been described as the “world’s strongest concentration of youthful rhyolitic volcanoes” in what is the “largest and most frequently active rhyolitic magmatic system on earth” (Newnham et al. 1999). There is a linear series of active volcanoes from Mount Ruapehu in the central North Island northwards to White Island in the Bay of Plenty. The main centre of activity was in what is now northeastern Lake Taupo, where at least 29 separate major eruptions are on record over a period of 50,000 years, during which it is estimated that 10,000 km³ of tephra were discharged. The largest of these was the Kawakawa eruption, when more than 800 km³ of tephra were ejected, reaching an estimated elevation of 20 km. Ash from this eruption has been reported widely around New Zealand, including Nelson/Marlborough and the Grey River Valley on the West Coast of the South Island, and also the Chatham Islands >800 km to the east. This eruption took place at about the time of the last substantial glacial advance.

The last major Taupo eruption, variously timed at AD c.186–280, has been described as the most powerful and violent volcanic event in the world in the past 5,000 years, or in recorded ‘human history’. Material discharged at that event has been estimated as 104 km³. The eruption column reached a height of 6 km, and atmospheric dispersion of the ash resulted in changes in the colour of the sky that were documented in both China and Rome. Ash from New Zealand volcanism has been reported from deposits in Greenland (Wilson and Houghton 1993; Wilson and Walker 1985; Horrocks and Ogden 1998).

Volcanic activity was also ongoing, elsewhere, though of a rather lesser scale, with one most recent, substantial eruption event that was based in Mount Tarawera in 1886. There are continuing, intermittent minor eruptions from the central North Island volcanoes of Ruapehu, Tongariro, and Ngauruhoe, and also White Island in the Bay of Plenty, in present times. In contrast with most major South Island lakes being an outcome of glaciation, many of the lakes in the North Island are largely an outcome of volcanism, and were formed either by collapsed calderas or explosion centres (see Lowe and Green 1987; Mosley 2004; Williams and Keys 2008).

Residual biogeographical impacts of volcanism are most likely to relate especially to:

- (i) The major Taupo eruptions, the last around AD 186.
- (ii) Mt Taranaki about AD 1700.
- (iii) Probably some of the volcanic activity around Auckland – though siting of Auckland city in this area may have obliterated (or substituted for!) much of the biotic disruption of volcanism.

- (iv) Mount Tarawera in 1886, where Stafford (1986: 253) told of local volcanism in which Lake Rotokakahi in the Bay of Plenty suddenly rose in temperature, “gradually turned a most peculiar, intense, vivid pea green colour and ... many thousands of dead and dying fish ... were swept down the creek and cast gasping on the shore.”
- (v) Continual, contemporary discharge of toxic materials from central North Island volcanoes into streams that drain them radially, especially headwater tributaries of the Whangaehu, Whanganui, and Waikato Rivers (Woods 1964; Sheppard 1996; Spiers and Boubée 1997; Chisnall and Keys 2002; Edgar 2002; Williams and Keys 2008). Deely and Sheppard (1992) found that even in the sea near the estuary of the Whangaehu River, in the southwestern North Island, heavy metal concentrations were higher than in industrially polluted waters elsewhere in New Zealand, this being a direct outcome of ongoing Central North Island volcanism.

Clarkson (1990) reckoned that volcanic activity has influenced the vegetation over an area of c. 20,000 ha in the North Island for the past 450 years, this being both much later than the massive AD 186 Taupo eruption, as well as involving much less severe activity. Clearly, volcanism in the central North Island has been enduring, pervasive, and of substantial historical and ecological biotic/biogeographical significance, including major impacts on freshwater ecosystems, some of which can still be identified in the distribution patterns of certain freshwater fishes (Lowe and Green 1987; McDowall 1996; Mosley 2004).

Judging by the effects of some relatively minor contemporary volcanic eruptions in both New Zealand and overseas (Bisson et al. 1988; McKnight and Dahm 1990; McDowall 1996), the impacts of the earlier, repeated major eruptions on the quite small New Zealand landscape must have been quite cataclysmic, and of particular present relevance, including major impacts on waterways, both rivers and lakes, and the life they support. Much of the North Island was covered with ash at various eruptions. Sometimes, ash discharges from the Taupo eruptions were blown and deposited to the east and northeast by prevailing westerly and south-westerly winds, but there were certainly effects in all directions (Fig. 3.5). Whole river systems would have been affected by erosion of ash deposits, both spatially as well as temporally. Rivers draining land both within the area where the ash was deposited, as well as downstream as far as the river mouths, would have experienced massive enduring, erosion of toxic ash deposits, and these impacts would have been felt even at sea (Carter 1994), at least, and perhaps especially, in close proximity to river mouths. Over a wide radius, river systems like the Waikato, Waihou, the Rotorua lakes and Kaituna and Tarawera Rivers, the Whakatane, Rangitaiki, Motu, Mohaka, Ngaruroro, Rangitikei, Turakina, Whangaehu, and Whanganui Rivers, and probably others, would have continued to carry ash downstream for decades after each major eruption event. This would have persisted at least until terrestrial plant communities became established and so stabilised soil surfaces on the ash-covered landscape (Newnham et al. 1999, suggested that this took about 300 years), but riverine effects probably would have lasted much longer as, even today, serious

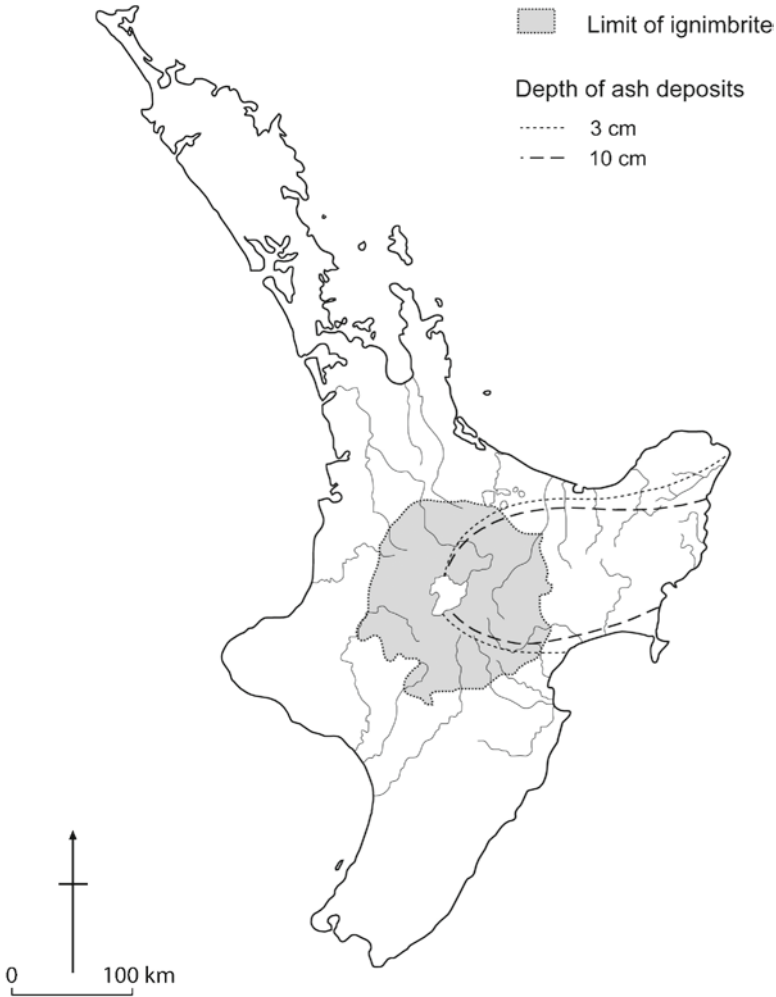


Fig. 3.5 The North Island of New Zealand showing the spread of ignimbrite and ash deriving from the c. 186AD Taupo eruption

flooding in the tributaries of Lake Taupo causes substantial erosion of old tephra deposits that have adverse impacts on aquatic biotas (Tombs 1960; Deely and Sheppard 1992; Cronin et al. 1997; Spiers and Boubée 1997; Manville et al. 2007). Similarly, chronic and event-based discharges of toxic water from volcanic crater lakes continue to affect some stream biotas. A major lahar burst from the crater lake of Mount Ruapehu in March 2007. There have been 13 such discharges since 1945, and another major one in 1953.

Probably, it is the biotic effects of the more recent volcanic eruptions on a broad swath of the North Island, from the central North Island volcanoes, across the Taupo

volcanic zone, through to the Rotorua area, and further out to sea in White Island, that persist most strongly, and aquatic impacts probably most especially in some of the upper tributaries of the Whangaehu River (Cronin et al. 1997). However, residual biogeographical impacts are likely, also, in the other various areas of recent volcanism, including the Auckland isthmus and around Mt. Taranaki. Biogeographic impacts following eruptions are likely to have been profound.

Throughout New Zealand there are also many lakes formed by earthquakes (often associated with the Alpine Fault – see red line in Fig. 2.1) that caused massive landslides, including some substantial lakes, like Waikaremoana, Tutira, Chalice, Christabel, Matiri and Gunn (Adams 1981; Lowe and Green 1987).

3.6 The Alpine Fault

Undoubtedly the other, most significant geological event/process/structure in New Zealand has been the Alpine Fault (see Fig. 2.1), which, of course, has been intimately connected with all of the geological processes discussed above. The fault lies over the boundary between the Australian Tectonic Plate to the west and the Pacific Plate to the east. Bilateral, horizontal movement of the plate boundary (described as “dextral strike/slip displacement”, by Wallis and Trewick 2009) has resulted in the displacement of rock formations that were formerly adjacent now being c. 480 km apart in the South Island; this movement of the fault continues and is the source of New Zealand's considerable vulnerability to earthquakes. It is commonly stated that movement continues at about the rate at which a human fingernail grows, or c 42 cm per year (Holdaway and Worthy 2006: 111; Craw and Norris 2003), and so is quite substantial.

3.7 Changes to Patterns of River Drainage

Disruption of the landscape, associated with the emergence of mountain ranges, the development of river catchments, and the formation of alluvial plains, is likely to have caused massive changes in New Zealand river systems. West-flowing river systems in the South Island, today, have much steeper gradients than east-flowing rivers at similar latitudes, in part because of the topography of the landscape, and perhaps also because most precipitation comes from the west. As a result, western river systems have tended to capture the headwaters of eastern flowing rivers (Craw et al. 2008). Rivers carrying sediment to the west have not formed alluvial plains like those flowing east and north-east. Numerous changes in fluvial connections between river systems are known, and some of these have already been shown to have had significant biogeographical influences. Many others no doubt await discovery. Some instances are:

- (i) The Waikato River alternated, perhaps as many as four times (Selby and Lowe 1992) between flowing to the west coast of the North Island, as now, or north through the Hinuera Gap into the Hauraki Gulf.
- (ii) There were once connections between rivers draining the south-western North Island (the area from around Wanganui south to the coastline north of Wellington) with others draining from the northern South Island (Tasman Bay and the Marlborough Sounds (Fleming 1979).
- (iii) The Kaituna River in Marlborough once flowed south into the Wairau River, but now flows north into Pelorus Sound (Mortimer and Wopereis 1997; Waters et al. 2006).
- (iv) Former headwater tributaries of the Lewis River, near the Lewis Pass were captured by the Maruia River in the west-flowing Buller River system (Soons 1992).
- (v) There were complex changes in the headwaters of the Wairau and Clarence Rivers in inland Marlborough that altered flow directions; the upper reaches of the Wairau once flowed into the Severn River (now a tributary of the Clarence River), but after retreat of glacial ice following the peak of the last (Otiran) glaciation, the Wairau River headwaters were diverted away from the Severn/Clarence catchment, into their present drainage pattern constituting the upper tributaries of the Wairau (McAlpin 1992; Smith et al. 2003).
- (vi) The Waimakariri River, which now flows east to the sea north of Banks Peninsula, may once have headed further south across the Canterbury Plains, joining the Selwyn River, and flowing to sea south of Banks Peninsula, and roughly where Lake Ellesmere is now present (Kirk 1994).
- (vii) A dramatic example of western capture is the Landsborough River in South Westland – which was once connected to the east-flowing Hunter River in what is now the upper Clutha River (headwaters of Lake Wanaka), but was captured by headwaters of the west-flowing Haast River; these rivers are now separated by a 1,900 m high mountain ridge (Craw et al. 1999, 2008; Cooper and Beck 2009).
- (viii) The Cardrona River formerly flowed south into the Kawarau River, but now flows north into the upper Clutha a little east of the origins of that river in Lake Wanaka (Craw and Norris 2003; Craw et al. 2007).
- (ix) The Nevis River, now flows north into the Kawarau, a major inland Clutha River tributary, but once flowed south into the Maitai (Craw and Norris 2003).
- (x) The Von River, which now drains north into Lake Wakatipu, formerly flowed south to join the Oreti, perhaps as recently as 5,000 years ago (Craw and Norris 2003).
- (xi) The southern arm of Lake Wakatipu formerly joined the Maitai, flowing south but, following amelioration of climate and glacial retreat in the late Pleistocene, the southern outlet of what is now Lake Wakatipu, via the Maitai River, was blocked by glacial moraine, and the outflow from Lake Wakatipu began to discharge eastwards (as now) through the Kawarau River in the upper Clutha River system (Craw and Norris 2003).

- (xii) There were probably old connections between the various of the upper tributaries of the Waiau, Oreti and Mataura Rivers in the upper (inland) slopes of the Southland Plains (Craw et al. 2008).
- (xiii) The headwaters of the Taieri River presently flow south; could they, or part of them, once have flowed more west to join the Manuherikia River, part of the Clutha River system?
- (xiv) There may also once have been connections between the upper Manuherikia River (Clutha River system) and the upper Ahuriri River (Waitaki River system) to the north.

There are undoubtedly many other, undiscovered, instances of more local and less radical changes in riverine flow patterns. Wellman and Willett (1942) discussed several local changes in south Westland, as did Vella et al. (1987) in the headwaters of the Mangahao and Mangatainoka in the upper reaches of the southern arm of the Manawatu River, in the Wairarapa, in the southeastern North Island. Also, the Waiohine, which formerly drained directly into Lake Wairarapa, relocated its discharge further east into the Ruamahanga River. A more contemporary change involved the Waitangi-taona River, on the West Coast of the South Island, which formerly went directly to sea, but relocated during a major flood event in 1967 (Soons 1992), and now flows through Lake Wahapo, and ultimately to sea via Okarito Lagoon, as it still does.

Such captures of river headwaters by other rivers flowing in different directions are bound to have had interesting implications for understanding some fish distribution patterns, discussed later in this book, though they need also to be understood in the context of other influences such as the cycles of glaciations, especially in the western South Island.

Thus several independent, but variously concurrent, geo-climatic processes seem likely to have profoundly affected the terrestrial/freshwater biota of New Zealand:

- Changes in landscape area generated by rising and falling sea levels.
- Changes in topography driven by tectonic processes – especially uplift of major mountain ranges and their erosion to form flood plains.
- The impacts of volcanism over a wide geographical area and across long geological time scales.
- Changes in the connections between river systems.
- Changes in climate, as during the cooling in the late Miocene, and then the later Pleistocene glacial periods.

These processes make Heads and Patrick's (2003) assertion that species have tended to "stay put" over long geological time scales in localities where they are now present, seem simply silly; the various geological and climatic events discussed above suggest that throughout the Cenozoic to Recent of New Zealand, there has been a very active process of local extirpations, dispersals, and re-invasions across the landscape, driven by the continual and diverse geological and climatic events described above – emergence and submersion of land,

mountain building and erosion, glacial advances and retreats (and climate change), volcanism, and changing land and river connections, as well as major climate changes. These would have allowed, provoked, or required, major redistribution and invasions by a broad range of plant and animal species, freshwater fishes among them, constituting a significant aspect of New Zealand's historical biogeography.

As noted above, New Zealand's mountains are substantially a consequence of the meeting of the Pacific and Australian Plates, with the Pacific Plate being subducted beneath the Australian one (Campbell and Hutching 2007) and they are relatively young (mostly Pliocene or more recent) (Kamp 1992; Craw et al. 2008).

3.8 Indications of an Ancient Biota

Though there have been frequent assertions that the New Zealand biota has ancient origins that indicate a Gondwanan ancestry, few of these have provided careful and convincing accounts of the dates of connections between biotic elements in New Zealand and other southern lands. From a biogeographical perspective, details of New Zealand's transformation during the early Cenozoic are undoubtedly dominated by a period of extensive marine transgression in the early Oligocene (c. 35 mya), when emergent New Zealand was certainly reduced to a series of relatively smaller islands, thought by some, together, to comprise less than 20% of the present land area (Fig. 3.2: Fleming 1979; Cooper and Cooper 1995), or c. 54,000 km². Others, however, postulate that even less and perhaps none of it survived this marine transgression (Campbell and Hutching 2007; Landis et al. 2008), and this has been an interesting, ongoing debate.

There is, I think, some evidence contrary to a complete submergence. Apart from the dinosaurs, discussed above (and see Molnar and Wiffen 1994; Wiffen 1996), it has been suggested that some bird groups, such as the New Zealand wrens (f. *Acanthisittidae*), and perhaps the kakapo, a large, flightless nocturnal parrot (*Strigops*) have ancient heritages in New Zealand. In particular, the *acanthisittids* sit at the very base of the large passeriform bird radiation, and the family is distinctly New Zealand (Ericson et al. 2002), and seem to demand continuous land somewhere in New Zealand. As discussed earlier, Stockler et al. (2002), Knapp et al. (2005) and Lee et al. (2008) have all suggested that aging of the presence of the araucarian tree *Agathis* indicates an ancient ancestry in New Zealand dating from prior to the hypothesised Oligocene drowning, though these conclusions could also be misled by extinctions of more recent relatives elsewhere, and this is a difficulty that could potentially apply in other instances, and is very difficult to evaluate.

Another aspect of the question of a vicariant New Zealand biota is that if some of New Zealand did remain emergent throughout the Oligocene drowning, the surviving, emergent islands involved were probably small. As the emergent land increased substantially in area following maximal submergence, there might have been substantial radiation in some animal groups, as seems possible for the more

than ten species of moa (f. *Dinornithidae*), the many geckos and skinks (ff. *Geckonidae* and *Scincidae*), and perhaps also for the galaxiid fishes, among others. If that is what did happen it would be near impossible to distinguish a radiation based on an ancient taxon that survived through the Oligocene from one based on post-Oligocene dispersals to New Zealand from elsewhere. In all probability some of both could have taken place, and the repeated identification of radiations soon after the Oligocene does not, in itself, necessarily indicate recent arrival. It could mean survival of relicts that later diversified.

Some workers have discussed the prospect of a significant genetic bottleneck for the New Zealand biota at the time of maximum marine transgression/submergence (Fleming 1979; Cooper 1989, 1998; Cooper and Millener 1993; Pole 1994, 2001), but if Landis et al. (2008) are correct it was not so much a bottleneck as extinction and replacement by subsequent dispersal with the likelihood of much presence of a founder effect (Mayr 1963). Genetically, it would sometimes be difficult to discriminate on the one hand between the limited gene pool resulting from the founder effect, and on the other the effects of a severe reduction in the size of the gene pool that might have resulted from a greatly reduced population size deriving, in turn, from a greatly reduced land area. Whichever scenario applies, McGlone et al. (2001) found little evidence for a Gondwana inheritance in the New Zealand, only supposition. For them, "early separation from Gondwana and subsequent complex Cenozoic history of subsidence, mountain building, large-scale fault movement, volcanism and climate change provide support for a rich array of biogeographical hypotheses."

A variety of authors, working on a diverse array of taxonomic groups, do argue for continuous land of some sort, presumably inhabited by a diverse fauna and flora. In perhaps the most explicitly detailed case, Boyer and colleagues (Boyer et al. 2007; Boyer and Giribet 2009) described the Pettalidae, a family of opiliones (*Arachnidae*), as a very ancient group, and argued that its distribution indicates an ancient, Gondwana range – reporting the family from Australia, Madagascar, New Zealand, South Africa, southern South America and Sri Lanka, this being a "...temperate (southern circum-Antarctic Gondwana clade containing all members of the Pettalidae ...)" They described this group as being "positioned at the base of a radiation dating back 178–215 million years", and they identified three distinct monophyletic groups in New Zealand, each with its closest relatives elsewhere on other formerly Gondwanan lands. This, in their view "contradicts the idea of recent dispersal to New Zealand," though, of course, the dispersal would not have to be 'recent', and could as easily be early Cenozoic. They concluded that "Despite the lack of precise dating, the history of Cyphophthalmi in New Zealand has clearly been influenced by ancient Gondwanan vicariance," and that "The family represents a distinctive example of a Gondwanan group whose distribution may indeed be explained solidly by vicariance...a circum-Antarctic clade of formerly temperate Gondwana species..." They argued that "if the New Zealand species were nested in Australian genera, then dispersal would be indicated, but they are not." Boyer et al. (2007) made an *a priori* assumption that these arachnids cannot disperse across oceans for reasons they did not explain, though Boyer and Giribet

(2009) later described the group as occurring in the moist litter of forests and showed that it is not present on any of the southern oceanic islands. On these grounds, they argued against the likelihood of transoceanic dispersal. The facts that the family is present in so many Gondwanan lands, is found only in such lands, and is absent from young islands where dispersal would be required for their presence, is certainly informative and consistent with a lack of waif dispersal. So, Boyer and her colleagues may be right: The Pettalidae may be a genuinely ancient Gondwanan group. Incomprehensibly, Boyer and Giribet (2009: 1,095) state that “New Zealand was the **last** major land to separate from temperate Gondwana” (present author’s emphasis), and this can only be an inadvertent error (if perhaps a Freudian one).

In addition, Worthy and Holdaway (2002) insist that “... a terrestrial fauna could always [have found] a home somewhere in the New Zealand archipelago,” and certainly, there are some elements in the New Zealand biota that would not easily have reached New Zealand across substantial oceanic gaps. These are not necessarily the same elements as are more usually described as unlikely to have dispersed, such as *Nothofagus* beech trees and the tuatara. I am thinking more of: the freshwater crayfish, *Paranephrops* and its temnocephalid commensal (McDowall 2005); the freshwater mussel, *Echyridella*; perhaps the frog genus *Leiopelma*.

Interestingly, Wilson (2008) showed that a New Zealand/Australian clade of often hypogean freshwater phreatoicid amphipods has a shared ancestry dating back >130 million years, and he claimed that this was consistent with “a subterranean freshwater fauna surviving the presumed Oligocene inundation of New Zealand.... The presence of a clade of blind Phreatoicidae in south-eastern Australia and New Zealand, but the absence of all sighted Phreatoicidae in New Zealand, supports a[n] hypothesis that subterranean freshwater refuges were present during the Oligocene flooding of New Zealand.” Perhaps ironically, for these animals to have lived in subterranean habitats it would seem necessary that a part of the New Zealand land surface was emergent. We could add peripatus, turbellarians, leeches, annelid earthworms and other groups to the above list, and perhaps many more. Note that the taxa that I list above are often freshwater organisms, or they have a close association with moist habitats (McDowall 2008). Gibbs (2006) listed the freshwater insect genus *Nannochorista*, another freshwater organism, as an ‘emblematic’ Gondwanan biotic element in New Zealand, the inference being that it predates the Oligocene drowning in New Zealand, and it, too is a freshwater organism, though it does have a flighted, terrestrial adult.

Worthy et al. (2007) show that there was a diverse, rich and highly endemic bird and other terrestrial/freshwater fauna present at St Bathans in Central Otago in the early Miocene, and they argue strongly for a fauna there that then had “a strongly New Zealand flavour to it.” On that basis they concluded that a “diverse terrestrial vertebrate fauna [must have] passed through the postulated Oligocene bottleneck.” The presence of a crocodilian, the swiftlet *Collocalia* sp. and probably abundant parrots are in keeping with a subtropical environment reconstructed from macro- and micro-floral studies (Pole et al. 2003). Most recently, Jones et al. (2009) have reported a skeletal fragment of the tuatara, *Sphenodon* (Rhynchocephalia), from the Miocene of Central Otago and have argued, I think persuasively, that this suggests

continuous emergent land somewhere in the New Zealand region since its late Cretaceous separation from Gondwana. And Worthy et al. (2009) again argued for the presence of a distinctive and substantial fauna in New Zealand early in the Miocene, which implies a prolonged earlier presence there.

So, the question of how much of Zealandia disappeared beneath epicontinental seas in the Oligocene is going to continue to be argued, and certainly there is no explicit evidence to support a complete drowning of proto-New Zealand during this period of high sea levels as suggested by Campbell and Landis (2001).

The interpretation of New Zealand biogeography must therefore be undertaken in the context of these multiple, geological and biogeographical processes and influences and, regardless, New Zealand's biota certainly has a derivation strongly influenced by continual transoceanic dispersal across very long time scales. Whether or not New Zealand did submerge entirely, as Holdaway and Worthy (2006: 122) put it, there was certainly a "... continuous 'rain' of potential colonists that undoubtedly existed throughout the Tertiary and continued into the Holocene...", i.e., transoceanic dispersal, and it is still happening!

3.9 The Evolution of an Alpine Biota

As discussed earlier, New Zealand now has substantial mountain ranges (to >3,500 M) with extensive permanent snow fields and glaciers, especially in the South Island, and these are inhabited by a distinctive alpine biota that has generated much discussion and some controversy (Dawson 1963; Burrows 1965; Wardle 1963, 1968, 1978, 1991; Raven 1973; Fleming 1979; McGlone 1985; Wardle 1988, Winkworth et al. 2005; Gibbs 2006). Cockayne (1928) argued that the alpine flora is derived from endemic elements dating back to Cretaceous times. However, as all of the major mountain ranges, including the Southern Alps of the South Island, were formed very much later than that, during or since the Pliocene (Fleming 1979; Stevens 1980; McGlone 1985; Whitehouse and Pearce 1992; Campbell and Hutching 2007), there would have been little or no New Zealand alpine landscape earlier during the Cenozoic, and so there could have been little or no specialised early Cenozoic alpine biota, either (Trewick et al. 2000). Moreover, we face, once more, the complication that certainly most, and perhaps all, of the New Zealand landscape was submerged by epicontinental seas in the Oligocene (Cooper and Cooper 1995; Cooper 1998; Campbell and Hutching 2007; Landis et al. 2008), providing little or no scope for the survival of any terrestrial biota, and what there was would not have been alpine in character. Moreover, the early-mid Miocene was a period of substantially higher temperatures than now (Campbell and Hutching 2007; Jones et al. 2009). The uplift of mountain ranges during the late Pliocene, Pleistocene, and continuing, would have caused decline in temperatures in the increasingly elevated areas. And, as well, and at the same time, the long series of episodes of severe climatic cooling associated with Pleistocene glaciations would have been an additive climatic/temperature influence, greatly increasing the area

and diversity of alpine conditions available – extending these to lower elevations at glacial maxima, while excluding all life from higher elevations, where there would have been very extensive seasonally-permanent ice or snow cover, especially in the South Island. How, then, could biotic elements possibly have “stayed put” (Heads and Patrick 2003).

Wardle (1978) considered that the alpine flora of New Zealand has developed largely since the Pliocene and that this was consequential to the formation of the mountain ranges, though he did argue that earlier habitat diversity in New Zealand might have been rather greater than “is implied by the usual picture of a low-lying sub-tropical archipelago” of the mid-Cenozoic. Fleming (1979), similarly, proposed that the modern alpine zone of New Zealand was probably established as recently as the Pleistocene, so that the “New Zealand plants and animals now endemic to the Alpine Zone have had only a [relatively] short existence as alpine in New Zealand”. Winkworth et al. (2005) summarised that some of the Recent to Present alpine flora evolved from lower elevation elements driven to cold tolerance by the Pleistocene glaciations, or at least biotic elements that were sorted for temperature preferences or tolerances, some of them derived by dispersal from other cool-cold southern lands, especially Andean South America, while a few probably even resulted from very long-distance dispersal from as far away as cold Northern Hemisphere floras.

Cold adaptedness certainly would have begun to evolve among local biotic elements as a result of glaciation, from the earliest cooling episodes, and especially at more southern latitudes. The species would presumably have migrated down- and up-slope as colder glacial periods waxed and waned, or some would have become more cold-adapted where they couldn’t move. Some naturalists have argued for widespread local extinctions, and then reinvasions from further afield (Burrows 1965; Wardle 1963). McGlone (1985), however, concluded that the series of “at least 20 [Pleistocene] glacio-eustatic sea level cycles...gave rise to a pattern of cool and largely deforested periods alternating with warm mild episodes, during which the forest cover was near complete”. The biogeographical implications of the long series of alternating Late Pliocene-Pleistocene glacial advances and retreats seem likely to be most explicitly reflected in today’s flora, as the likely outcomes of the most recent Otiran glaciations (c. 100,000–10,000 years ago, with at least three interstadials and the last glacial maximum c. 25–15,000 years ago – Soons 1979; McGlone 1985). In part this is simply because the latest advances are likely to have, at least, modified or even substantially obliterated or overwritten earlier impacts from similar events. Though there is debate about how these effects can be identified in present biotic distributions, it can probably be concluded that a substantial alpine-adapted biota was available to occupy the higher inhabitable elevations as the last glaciation receded to produce the alpine biota and its distribution patterns seen today.

McGlone (1985) estimated that it took about 500 years for restoration of forest in the South Island when climate ameliorated and the ice retreated, and he proposed that localised and widespread Pleistocene refuges were the likely sources for reinvasions of plant associations, especially forest, when climate became warmer.

When warming climates drove cold-loving taxa to higher elevations, there would have been substantial scope for geographical separation of lineages, isolated on the various mountain ranges and peaks, or others within the intermontane valleys. There may also have been north/south displacement of various biotic groups to accommodate climate change, as well as upslope and downslope displacement. Temperature changes would have had greatest impacts on stenotherms, such that rising temperatures would have had seriously adverse impacts on cold stenotherms that were already southern in range, or on warm stenotherms that were already northern, and which in both instances had nowhere to go as climate changed. Inevitably, some taxa would have become trapped in local climatic pockets from which they could not escape, and as a result have disappeared from the local biota – though we know little or nothing about such events and processes, especially as regards the freshwater fish fauna. However, what does seem likely is that any additions to the cold-adapted fauna among the freshwater fishes would probably have been locally evolved. New Zealand's galaxiids, in particular, are cold-tolerant, and would have been well adapted to coping with the thermal stresses of glaciation. There has been virtually no previous discussion of the implications of these various geological and climatic events for riverine biota, but the massive filling with ice (sometimes many hundreds of metres thick) of the big, intermontane eastern valleys of the Southern Alps (Willett 1950; Gage 1958), in particular, indicates that the riverine habitats now found in the sub-alpine to intermontane valleys, as well as their present biotas, are quite recent. Members of the 'pencil-galaxias' species complex, in particular, favour higher elevation and cold habitats and probably followed the retreating glacial landscapes and waterways inland and upslope as temperatures ameliorated following the last glacial retreat. Various of them are found today in fluvial habitats upstream of the glacial lakes that formed in association with this retreat (see Chapter 12).

3.10 The Place of New Caledonia

Although this book is about New Zealand, New Caledonia (see Fig. 1.1) is a largish island that is well accepted as a part of the mini-continent Zealandia, of which New Zealand is the largest presently emergent land surface. Therefore, some mention of New Caledonia and its biogeographical history is appropriate here. Grandcolas et al. (2008: 3,310) found New Caledonia to be a "remarkable palaeogeographic model as it presents a combination of continental and oceanic [island] features", in much the same way as this has been suggested for New Zealand. There are some interesting contrasts and equally interesting similarities between the stories associated with these two old islands in the western Pacific.

New Caledonia is much more tropical, lying around 1,700 km north of New Zealand and 1,200 km east of central Australian latitudes (Grandcolas et al. 2008), and has present surface area of around 18,500 km², and so is very much smaller than New Zealand. Geologists have shown that "In the Palaeocene, the part

of Zealandia that became New Caledonia experienced lengthy submersion in deep water,” that this submersion may have lasted for more than 20 million years, and that it emerged during the Oligocene (Grandcolas et al. 2008), at which time New Zealand suffered its greatest and perhaps total submersion (Cooper and Cooper 1995; Landis et al. 2008). Grandcolas et al. (2008) concluded that this prolonged early Cenozoic submersion of New Caledonia makes it “difficult to retain the notion that a Gondwanan biota has survived” there, and it means that there must have been recolonisation following its emergence (as is argued for New Zealand by those who consider that it, too, was totally submerged). Grandcolas et al. pointed to “multiple, nested relationships involving taxa” from a variety of other locations, including Australia, New Zealand, Norfolk Island, Vanuatu, Indo-Malaysia, and even more widely.

Grandcolas et al. (2008: 3,313) have concluded that for New Caledonia apparently ancient groups such as the Araucariaceae (a genus of large coniferous trees), Proteaceae (a basal family of small dicotyledonous trees and shrubs), the genus *Placostylus* (a terrestrial gastropod mollusc), *Paratya* (a genus of amphidromous shrimps)... crickets, diving beetles, cockroaches...have spread by dispersal, as often indicated by the presence of a few distinct clades estimated to be less than 15 Ma. – they discuss “deeply rooted and therefore relatively old groups occurring in distant parts of the world [and] frequently considered as relicts and used to support the likelihood of a New Caledonian biota of Gondwanan origins.” They propose arrival in New Caledonia by dispersal, which they consider to have been repeated and in many groups. *Araucaria* they thought to have been present for less than 10 Ma, but Proteaceae for rather longer, probably from soon after re-emergence, and so about 40 Ma. They found no unambiguous evidence for any very ancient Gondwanan representation, but rather that a variety of relatively old Gondwanan groups are represented in New Caledonia by species of quite recent origin, and consistent with the geological observations implicating submersion. Moreover, they found that in general Gondwanan origins of the New Caledonian biota are contradicted by both geological evidence and biogeographical/phylogenetic studies, in both of which the biota is dated as no older than Oligocene, and so later than the New Caledonian submergence. I discussed in an earlier section (Section 3.8) the ostensibly ancient Gondwanan distribution of the mite harvestmen (family Pettalidae) as proposed by Boyer et al. (2007) (Boyer and Giribet 2009), and it is of some interest and relevance that these authors do not mention Pettalidae as having been recorded from New Caledonia, despite the family’s presence on many formerly Gondwanan lands.

Heads (2008) has presented an account of the biogeography of New Caledonia, in which he connected the distributions of many pivotal taxa to highly intricate details of the landscape and geology of the island, ostensibly across very long time periods. Both he and Grandcolas et al. (2008) could not, I suspect, be correct, and even if New Caledonia did not totally submerge, I rather think that many of the associations discussed by Heads are inconsistent with the island’s historical geology.

Grandcolas et al. (2008) suggest that there is no evidence for direct biotic exchange of New Caledonia with New Zealand, but only the prospect of some stepping stone dispersal after re-emergence. Some have suggested that there may, at times, have been a chain of islands that provide a topographically and temporally partial connection between the two major islands (McLoughlin 2001; Lee et al. 2001) and that this may have been pivotal in mediating the biotic similarities between them and therefore important to New Zealand biogeography. There are several significant biotic elements implicated, such as *Nothofagus* (Swenson et al. 2001a, b; Knapp et al. 2005), araucarians (Knapp et al. 2007), cicadas and lizards (Chambers et al. 2001), but, according to Grandcolas et al. (2008), the island's entire biota can only have resulted from a total recolonisation, by dispersal, since the Oligocene.

It seems to me that one of the interesting and relevant aspects of New Caledonian biogeography has been the survival there of some enigmatic biotic elements. One example is the kagu, *Ryncochetos jubatus*, thought by some to be related to the extinct adzebills of New Zealand (family Aptornithidae) (Grandcolas et al. 2008). Another distinctive element in the New Caledonian fauna is the freshwater *Protogobius attiti*, the most primitive known gobioid fish, which possesses a complete lateral line, unlike other gobioid fishes (Watson and Pöllebauer 1998) and, as such, a sister taxon to a very large group of fishes with more than 2,000 species recognised (Nelson 2006). Its presence in New Caledonian fresh waters is of some interest, if we accept that the island was entirely submerged by sea in the early Cenozoic.

Grandcolas et al. (2008: 3,311) concluded that “Contrary to...common reasoning, we submit that these [apparently ancient, rather relictual-looking] groups do not provide much biogeographical and temporal information since their relatives are either absent from the region around New Caledonia, or have a worldwide distribution. Their long-time survival as relicts in New Caledonia is an indirection assumption of many extinction events in neighbouring regions such as Australia or New Zealand.” The history of these groups in New Caledonia, though poorly known in detail, must related to dispersal processes if it is accepted that in early Cenozoic times New Caledonia was completely submerged by sea for several to many millions of years. Here again is an idea of great biogeographical interest and the source of much lively debate.

This is not the place to explore these distinctive biotic elements in detail, though what interests me is that as in New Zealand, there is in New Caledonia an assortment of apparently ancient and peculiar elements that have ‘hung on’ across millions of years and which give the island’s biota a distinctive character – comparable with what I formerly called New Zealand’s “‘Mona Lisas’ of the natural world...the few remarkable ‘bits and pieces’ that have survived the prolonged and severe filtering processes to which the [New Zealand] biota has been subjected to over the past c. 18 Myr...” (McDowall 2008) – the occasional, seemingly enigmatic taxa of uncertain relationships and derivations, represented in New Zealand by such taxa as the tuatara, *Sphenodon*, the *Leiopelma* frogs. As in New Zealand there are in New Caledonia similar surviving ‘bits and

pieces' that tend to be distinctive to that island. They perhaps give the appearance of being relictual survivors that have persisted in New Caledonia, but they are almost entirely different from those that persisted in New Zealand. These differences can be viewed as the result of the historic winnowing processes that geographically isolated biotas are subjected to across geological time. They are interesting in terms of the understanding and insights that they provide of diversity and relationships but are really little more than surviving, residual oddities in a biogeographical sense. Grandcolas et al. (2008: 3,309) concluded that "New Caledonia's biodiversity is not that of a continental island that has retained many ancient groups since its separation from the northeastern margin of Australia ca. 80 Ma, but an oceanic island with a composite biota dominated by neoendemism and disharmonic colonization, a 'Darwinian' island. The question now for biologists is not so much whether the biota is Gondwanan and ancient, but when and in what manner the modern biota assembled."

Looking briefly at the New Caledonian freshwater fish fauna, there are items of interest, additional to *Protogobius*, discussed above. One is the presence in New Caledonia of a single galaxiid, generally referred to as *Nesogalaxias neocaledonicus* (Fig. 3.6), though its placement in a distinct, monotypic genus is controversial (McDowall 1968; Serét 1997). Given the accepted early Cenozoic submersion of New Caledonia (Grandcolas et al. 2008), this fish must have dispersed to New Caledonia following its re-emergence. Galaxiids are cool/cold water fishes, and the New Caledonian species is found only at higher elevations in a small lake at the southern end of New Caledonia. It gives the appearance of 'hanging on' in the perhaps coolest freshwater environment available to fishes there. The fish is distinctive in general form, in comparison to other galaxiid fishes, but this probably reflects its benthic, lacustrine habit that is unusual across the family Galaxiidae. Resemblance to the Australian lacustrine/benthic genus *Paragalaxias* (McDowall 1998) is probably at best convergent. Genetic sequence studies based on mtDNA, suggest that the New Caledonian species is closest to the koaro, *Galaxias brevipinnis* (Waters et al. 2000), which is found in southeastern Australia, Tasmania, New Zealand, and the Chatham, Auckland, and Campbell Islands (McDowall 1990; McDowall and Fulton 1996). The koaro is diadromous, its juvenile life being spent at sea (McDowall 1990; McDowall et al. 1994), so that

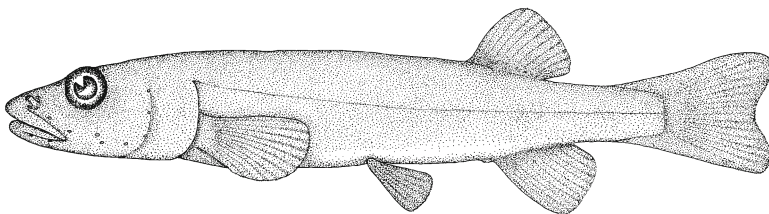


Fig. 3.6 *Galaxias neocaledonicus*, 52 mm LCF (family Galaxiidae) the distinctive relictual galaxiid from New Caledonia that probably has relationships to New Zealand/Australian *Galaxias* species

transoceanic dispersal to reach New Caledonia is quite conceivable (McDowall 2002), though whether it originated from Australia or New Zealand is presently unresolved. Otherwise, the New Caledonian freshwater fish fauna comprises a mixture of species that are largely amphidromous (especially sicydiine gobies) or catadromous (anguillid eels) that are characteristic of the islands of the tropical and sub-tropical Indo-Pacific, or are occasional stragglers that enter fresh waters from the seas around New Caledonia (Serét 1997; Marquet et al. 2003). In this sense, then, the New Caledonian galaxiid is highly distinctive in its southern, largely cool-temperate distribution – it perhaps connects biogeographically more closely with New Caledonian *Nothofagus* than it does with other freshwater fish found there (Marquet et al. 2003).

References

- Adams CJ, Campbell HJ, Griffin WJ (2008) Age and provenance of basement rocks of the Chatham Islands: an outpost of Zealandia. *N Z J Geol Geophys* 51:245–259
- Adams J (1981) Earthquake-dammed lakes in New Zealand. *Geol Today* 9:215–219
- Alloway BV, Neall VE, Vucetich GG (1995) Late Quaternary (post 28, 000 years B.P.) tephrostratigraphy of northeast and central Taranaki, New Zealand. *J R Soc N Z* 25:385–458
- Ballance PF, Williams PW (1992) The geomorphology of Auckland and Northland. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 210–232
- Bisson PA, Nielsen JL, Ward JW (1988) Summer production of coho salmon stocked in Mount St Helens streams 3–6 years after the 1980 eruption. *Trans Am Fish Soc* 117:322–335
- Boyer SL, Giribet G (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones; Cyphophalmi). *J Biogeogr* 36:1084–1099
- Boyer SL, Clouse RM, Benavides LR, Sharma P, Schwendinger PJ, Karunarathna I, Giribet G (2007) Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *J Biogeogr* 34:2076–2085
- Brook FJ (1999) Stratigraphy and landsnail faunas of Late Holocene coastal dunes, Tokerau Beach, northern New Zealand. *J R Soc N Z* 29:337–359
- Burrows CJ (1965) Some continuous distributions of plants within New Zealand and their ecological significance: Part II. Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. *Tuatara* 13:9–29
- Campbell HJ, Hutching G (2007) *In search of ancient New Zealand*. Penguin, Auckland, N Z, 238 pp
- Campbell HJ, Landis CA (2001) New Zealand awash. *N Z Geograph* 51:6–7
- Campbell HJ, Twreck S (2003) The Chatham Islands – Noah's ark or Picton Ferry. *Marsden Fund Update* 25:4
- Campbell HJ, Andrews P, Beu AG (1993) Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. *N Z Inst Geol Nucl Sci Monogr* 2:1–269
- Carter L (1994) Ocean sediment studies: volcanic eruptions – how big is big? *Water Atmos* 2(1):21
- Chambers GK, Boon WM, Buckley TR, Hitchmough RA (2001) Using molecular methods to understand the Gondwana affinities of the New Zealand biota: three case studies. *Aust Bot* 49:377–387
- Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Mol Phyl Evol* 52:470–487

- Chisnall B, Keys H (2002) Shortfinned eel found in the acidic Whangaehu River, Mount Ruapehu. *DOC Sci Internal Ser* 64:1–9
- Clarkson BD (1990) A recent review of vegetation development following recent (<450 years) volcanic disturbance in North Island, New Zealand. *N Z J Ecol* 14:59–71
- Cockayne L (1928) The vegetation of New Zealand. Engelmann, Leipzig, Germany, 456 pp
- Cooper AF, Beck RJ (2009) River capture and main divide migration in the Haast River catchment assessed from the fluvial distribution of sodalite-bearing dike rocks and fenites. *N Z J Geol Geophys* 52:27–36
- Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proc R Soc, Lond B (Biol Sci)* 261:293–302
- Cooper RA (1989) New Zealand tectonostratigraphic terranes and panbiogeography. *N Z J Zool* 16:699–712
- Cooper RA (1998) The Oligocene ‘bottleneck’ hypothesis – physical parameters. *Geol Soc N Z Misc Publ* 97:19–22
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 17–34
- Craw D, Youngson JH, Koons PA (1999) Gold dispersal and placer formation in an active, oblique collisional mountain belt, the Southern Alps, New Zealand. *Econom Geol* 94:605–614
- Craw D, BurrIDGE CP, Waters JM (2007) Geological and biological evidence for drainage reorientation during uplift of alluvial basins in Central Otago, New Zealand. *N Z J Geol Geophys* 50:367–376
- Craw D, BurrIDGE CP, Upton P, Rowe DL, Waters JM (2008) Evolution of biological dispersal corridors through a tectonically active mountain range, New Zealand. *J Biogeogr* 35: 1790–1802
- Cronin SJ, Hodgson KA, Neall VE, Palmer AS, Lecointre JA (1997) Ruapehu lahars in relation to the Holocene lahars of the Whanganui River, New Zealand. *N Z J Geol Geophys* 40: 507–520
- Dawson JW (1963) The origins of the New Zealand alpine flora. *Proc N Z Ecol Soc* 10:12–15
- Deely J, Sheppard D (1992) Heavy metals in the Whangaehu River: an example of a naturally contaminated river. Trace elements: roles, risks and remedies. In: *Proc N Z Trace Elements Group Conf*, Massey University, N Z, pp 41–51
- Douglas BJ (1986) Lignite resources of Central Otago: Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessments and exploration models. *N Z Energy Res Devel Comm Publ* 104:1–368
- Edgar NB (2002) Sustainable catchment management: a role for volcanic eruptions? *Verhand Int Verein theor ang Limnol* 28:1167–1171
- Ericson PGP, Chistididis L, Cooper A, Irestedt M, Jackson J, Johansson S, Norman JA (2002) A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc R Soc Lond B Biol Sci* 269:234–241
- Fitzharris B, Mansergh G, Soons JM (1992) Basins and lowlands of the South Island. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 407–423
- Fleming CA (1979) *The geological history of New Zealand and its life*. Auckland University Press, Auckland, N Z, 141 pp
- Gage M (1958) Late Pleistocene glaciations of the Waimakariri valley, Canterbury, New Zealand. *N Z J Geol Geophys* 1:123–155
- Gibbs GW (2006) *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton, Nelson, N Z, 232 pp
- Grandcolas P, Muriene J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: a very old Darwinian island. *Phil Trans R Soc Lond Biol Sci* 363: 3309–3317

- Heads M (2008) The panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basal terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *J Biogeogr* 36:2153–2175
- Heads M, Patrick B (2003) Biogeography. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. Otago University Press, Dunedin, N Z, pp 89–100
- Hill RS (1996) The riddle of unique Southern Hemisphere *Nothofagus* on southwest Pacific islands: its challenge to biogeographers. In: Keast RA, Miller SE (eds) *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*. SPB Academic, Amsterdam, The Netherlands, pp 247–260
- Holdaway RN, Worthy TH (2006) Evolution of New Zealand and its vertebrates. In: Merrick JR, Archer M, Hickey GM, Lee MSY (eds) *Evolution and biogeography of Australasian vertebrates*. Auscubus, Oatlands, N S W, Australia, pp 111–128
- Horrocks M, Ogden J (1998) The effects of the Taupo tephra eruption of c. 1718 BP on the vegetation of Mt Hauhangatahi, central North Island, New Zealand. *J Biogeogr* 25:649–660
- Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proc R Soc Lond B Biol Soc* 276:1385–1390
- Kamp PJJ (1992) Tectonic architecture of New Zealand. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 1–30
- Kirk J (1994) The origin of Waihora/Lake Ellesmere. In: Davies J, Galloway L, Nutt AHC (eds) *Waihora/Lake Ellesmere: past present future*. Lincoln University/Daphne Brasell, Lincoln, N Z, pp 9–16
- Knapp M, Stockler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beeches). *PLoS Biol* 3:38–43
- Knapp M, Mudaliar R, Havell D, Wagstaff SJ, Lockhart PJ (2007) The drowning of New Zealand and the problem of *Agathis*. *Syst Biol* 56:862–870
- Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA (2008) The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 143:173–197
- Lee D, Forsyth J (2008) Central rocks: a guide to the geology and landscapes of Central Otago. *Geol Soc N Z Guidebook* 14:1–84
- Lee DE, Bannister JM, Lindqvist JK (2008) Late Oligocene-Early Miocene leaf macrofossils confirm a long history of *Agathis* in New Zealand. *N Z J Bot* 45:565–578
- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust J Bot* 49:341–356
- Lees C, Neall V (1993) Vegetation response to volcanic eruptions on Egmont Volcano, New Zealand, during the last 1500 years. *J R Soc N Z* 23:91–127
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) *Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea Conference, Christchurch, New Zealand, 27–30 November, 1992*. Balkema, Rotterdam, The Netherlands, pp 119–137
- Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Mar Geol* 116:293–312
- Lowe DJ, Green JD (1987) Origins and development of the lakes. In: Viner A (ed) *Inland waters of New Zealand*. Department of Scientific and Industrial Research, Wellington, N Z, pp 1–64
- Manville V, Hodgson K, Nairn IA (2007) A review of break-out floods from volcanogenic lakes in New Zealand. *N Z J Geol Geophys* 50:131–150
- Marquet G, Keith P, Vigneux E (2003) *Atlas des poissons et des crustacés de Nouvelle Calédonie*. *Patrim Naturelles* 58:1–283
- Mayr E (1963) *Animal species and evolution*. Belknap Press, Cambridge, MA, 797 pp

- McAlpin J (1992) Glacial geology of the upper Wairau Valley, Marlborough, New Zealand. *N Z J Geol Geophys* 35:211–222
- McDowall RM (1968) The status of *Nesogalaxias neocaledonicus* (Weber and de Beaufort) (Pisces: Galaxiidae). *Breviora* 286:1–8
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1996) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1998) Phylogenetic relationships and ecomorphological divergence in sympatric and allopatric species of *Paragalaxias* (Teleostei: Galaxiidae) in high elevation Tasmanian lakes. *Environ Biol Fish* 53:235–257
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2005) Historical biogeography of the New Zealand freshwater crayfishes (Parastacidae: *Paranephrops* spp.): restoration of a refugial survivor? *N Z J Zool* 32:55–77
- McDowall RM (2008) Process and pattern in biogeography – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM, Fulton W (1996) Family Galaxiidae – galaxiids. In: McDowall RM (ed) Freshwater fishes of south-eastern Australia. Reed, Chatswood, N S W, Australia, pp 52–77
- McDowall RM, Mitchell CP, Brothers EB (1994) Age at migration from the sea of juvenile *Galaxias* in New Zealand. *Bull Marine Sci* 54:385–402
- McGlone MS (1985) Plant biogeography and the late Cenozoic history of New Zealand. *N Z J Bot* 23:723–749
- McGlone MS, Duncan RP, Heenan PB (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J Biogeogr* 28:199–216
- McKnight DM, Dahm CN (1990) Contribution of organic acids to alkalinity in lakes within the Mount St. Helens blast zone *Limnol Oceanogr* 35:535–542
- McLoughlin S (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Am J Bot* 49:271–300
- McSaveney MJ, Stirling MW (1992) In: Soons JM, Selby MJ (eds) Central Otago: basin and range country. Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 482–504
- Michaux B, Leschen RA (2005) East meets west: biogeology of the Campbell Plateau. *Biol J Linn Soc* 86:95–115
- Molnar RE, Pole M (1997) A Miocene crocodile from New Zealand. *Alcheringa* 21:65–70
- Molnar RE, Wiffen J (1994) Polar dinosaur faunas from New Zealand. *Cretac Res* 15:698–706
- Mortimer N (2004) New Zealand's geological foundation. *Gondwana Res* 7:261–272
- Mortimer N, Wopereis P (1997) Change in direction of the Pelorus River, Marlborough, New Zealand: evidence from composition of Quaternary gravels. *N Z J Geol Geophys* 40:307–313
- Mosley MP (2004) Rivers and the riverscape. In: Harding JS, Mosley MP, Pearson CP, Sorrell BK (eds) Freshwaters of New Zealand. New Zealand Hydrological Society/New Zealand Limnological Society, Christchurch, N Z, pp 8.1–8.18
- Neall V (1992) Landforms of Taranaki and the Wanganui lowlands. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 287–307
- Neall V, Treweek SA (2008) The age and origins of the Pacific islands: a geological overview. *Proc R Soc Lond Soc B Biol Sci* 363:3293–3308
- Nelson JS (2006) Fishes of the world 4th ed. Wiley, New York, 601 pp
- Newnham RM, Lowe DJ, Williams PW (1999) Quaternary environmental change in New Zealand: a review. *Progr Phys Geog* 23:567–610
- Pillans B, Pullar WA, Selby MJ Soons JM (1992) The age and development of the New Zealand landscape. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 31–62
- Pole M (1994) The New Zealand flora – entirely long distance dispersal? *J Biogeogr* 21: 625–635

- Pole M (2001) Can long distance dispersal be inferred from the New Zealand plant fossil record. *Aust J Bot* 49:357–366
- Pole M, Douglas B, Mason G (2003) The terrestrial biota of southern New Zealand. *J R Soc N Z* 33:415–426
- Raven PH (1973) Evolution of the subalpine and alpine plant groups in New Zealand. *N Z J Bot* 11:177–200
- Reay T (2003) Geology. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 3–16
- Sanmartin I, Ronquist F (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Syst Biol* 53:216–243
- Selby MJ, Lowe FJ (1992) The middle Waikato Basin and hills. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul Auckland, N Z, pp 233–255
- Serét B (1997) Les poissons d'eau de Nouvelle-Calédonie: implications biogéographiques de récentes découvertes. *Mem Mus Nat d'Hist Nat* 171:369–378
- Sheppard D (1996) The sterilisation of a river: ongoing volcanic pollution in the Whangaeu. *News N Z Geochem Group* 98:15–16
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tarndale bully revisited with molecular markers: an ecophenotype of the common bully *Gobiomorphus cotidianus* (Pisces: Gobiidae). *J R Soc N Z* 33:663–673
- Soons JM (1979) Late Quaternary environments in the central South Island of New Zealand. *N Z Geogr* 35:16–23
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 439–455
- Spiers D, Boubée J (1997) The effect of Ruapehu's ash on fish. *Fish Game N Z* 16:14–21
- Stafford DM (1986) The founding years in Rotorua: a history of events to 1900. Richards, Auckland, N Z, 448 pp
- Stevens GR (1980) *New Zealand adrift*. Reed, Wellington, N Z, 442 pp
- Stockler K, Daniel IL, Lockhart PJ (2002) New Zealand kauri (*Agathis australis* (D. Don) Lindl. Araucariaceae) survives Oligocene drowning. *Syst Biol* 51:827–832
- Suggate RP, Stevens GR, Te Punga MT (1978) *The geology of New Zealand*. Government Printer, Wellington, N Z, 2 vols
- Swenson U, Hill RS, McLoughlin S (2001a) Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. *Taxon* 50:1025–1041
- Swenson U, Backlund A, McLoughlin S, Hill RS (2001b) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* 17:28–47
- Tombs A (1960) Corrosion of metals in Whangaeu and Ruapehu crater waters. *N Z J Sci* 3:93–99
- Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Trewick SA, Wallis GP, Morgan-Richards M (2000) Phylogeographic pattern correlates with Pliocene mountain building in the alpine scree wet (Orthoptera: Anostomatidae). *Mol Ecol* 9:657–666
- Vella P, Neef G, Kaewyana W (1987) River piracy at Kakariki, northwestern Wairarapa, New Zealand. *J R Soc N Z* 17:373–386
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Wardle P (1963) Evolution and distribution of the New Zealand flora as affected by Quaternary climates. *N Z J Bot* 1:3–17
- Wardle P (1968) Evidence for an indigenous pre-quaternary element in the mountain flora of New Zealand. *N Z J Bot* 6:120–125
- Wardle P (1978) Origin of the mountain flora, with special reference to trans-Tasman relationships. *N Z J Bot* 16:535–550

- Wardle P (1988) Effects of glacial climates on floristic distribution in New Zealand. 1. A review of the evidence. *N Z J Bot* 26:541–555
- Wardle P (1991) *Vegetation of New Zealand*. Cambridge University Press, Cambridge, 672 pp
- Waters JM, Lopez JA, Wallis GP (2000) Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes: Galaxiidae): dispersal, vicariance and the position of *Lepidogalaxias salamandroides*. *Syst Biol* 49(4):777–795
- Waters JM, Craw D (2006) Goodbye Gondwana: New Zealand biogeography, geology and the problem of circularity. *Syst Biol* 55:351–356
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid fish lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Watson RE, Pöllabauer C (1998) A new genus and species of freshwater goby from New Caledonia with a complete lateral line (Pisces: Teleostei: Gobioidae). *Seckenb Biol* 77: 147–153
- Wellman H, Willett RW (1942) The geology of the West Coast from Abut Head to Milford Sound – Part 1. *Trans R Soc N Z* 71:282–306
- Whitehouse IE, Pearce AJ (1992) Shaping the mountains of New Zealand. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 144–160
- Wiffen J (1996) Dinosaurian palaeobiology: a New Zealand perspective. *Mem Queensland Mus* 39:725–731
- Willett RW (1950) The New Zealand Pleistocene snow line, climatic conditions, and suggested biological effects. *N Z J Sci Tech* 32B:18–48
- Williams K, Keys H (2008) *Ruapehu erupts*. Godwit, Auckland, 63 pp
- Wilson CJN, Houghton BF (1993) The Taupo eruption. Institute of Geological and Nuclear Sciences, Taupo, N Z, 6 pp
- Wilson CJN, Walker GPL (1985) The Taupo eruption, New Zealand. 1. General aspects. *Phil Trans R Soc Lond A314*:199–228
- Wilson GDF (2008) Gondwanan groundwater: subterranean connections of Australian phreatoid isopods (Crustacea) to India and New Zealand. *Invert Syst* 22:301–310
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ, Div Evol* 5:327–247
- Woods CS (1964) Fisheries aspects of the Tongariro power development project. *N Z Mar Dep Fish Tech Rep* 10:1–214
- Worthy TH, Holdaway RN (2002) *The lost world of the moa*. Canterbury University Press, Christchurch, N Z, 718 pp
- Worthy TH, Tennyson TADJ, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD (2006) Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proc Nat Acad Sci USA* 103:19419–19423
- Worthy TH, Tennyson AJD, Jones C, McNamara JA, Douglas BJ (2007) Miocene waterfowl and other birds from Central Otago, New Zealand. *J Syst Palaeontol* 5:1–39
- Worthy TH, Hand SJ, Lee MSY, Hutchinson M, Tennyson ADJ, Scofield RP, Marshall BA, Worthy JP, Nguyen MT, Boles WE, Archer M (2009) New Zealand's St Bathans fauna: an update of its composition and relationships. *Geol Soc N Z Misc Publ* 126:40–42

Chapter 4

A Conceptual Basis for Biogeography

Abstract Biogeographical patterns are an outcome of the combined influences of earth history and ecology. Dispersal has been of particular importance to the assembly of the New Zealand biota, the predominantly dispersal fauna being superimposed on any surviving residues of a biota already present when Zealandia separated from eastern Gondwana in the late Cretaceous. The relative roles of Gondwanan vicariance and dispersal in generating the biota have been robustly argued, but there is now a strong consensus that most of the modern biota has dispersal origins, with, at most, just a few relictual Gondwanan taxa. Some geologists argue for New Zealand being completely submerged in ocean in the Oligocene, though many biologists argue for some small emergent islands, based in part on evidence from DNA sequencing, the biological clock and also the low likelihood that some biotic elements could have dispersed across the sea. The implication of complete submergence is that the entire biota has dispersal derivations.

Keywords Biological clock • Cretaceous • Dispersal • DNA • Earth history • Geology • Gondwana • Marine submergence • Vicariance

4.1 The Basis for Species' Distributions

The geographical distributions of biological species are created by a complex amalgam of historical and ecological influences.

Species are *present* where they are:

- *Sometimes*, and partly, because that is where they originally evolved (their 'centre of origin').
- *Or* because they have been able to spread to/among the areas now occupied owing to the combined influences of evolutionary divergence, speciation and dispersal, or they would be not be present there.
- *And* because environmental conditions are now congenial, and have been, more or less, since the species reached their present ranges or, again, they would no longer be there.

Species' ranges are dynamic attributes, constantly changing in response to the challenges of all sorts of environmental variables – species shift elevations and/or move latitudinally at times of climatic warming or cooling, when some species are displaced from historic ranges; or terrestrial species vacate landscapes that become inundated by coastal seas that are then available to marine species; or they invade landscapes that emerge from marine or freshwater inundation and so become inhabitable by terrestrial organisms. Or, the limits of a species' range may shift simply as a result of dispersal when vagility is high or under the influence of ecosystem processes. These changing species' ranges have consequential impacts on community composition. Thus taxa undergo historical expansions, contractions, and range shifts that result from habitat changes and climatic variables, across a broad range of scales from global to local. Because of the huge geological time scales of these changes, much of the detail of ancestral distribution patterns, as well as the causes of the changes may now be hidden by history – the effects of early events being “overwritten” by more recent ones (Waters and Craw 2006). Present ranges are just the latest in a likely series of highly fluid and changing patterns across time and space.

Species are *absent* from areas for rather more diverse reasons. They are, of course, absent where environmental conditions are not now congenial, or where the species are incompatible with other components of the ecosystems, or essential concomitant taxa are missing (such as essential dietary items), but also species may be absent from areas where environmental conditions are now just as congenial to them as places where they are present: i.e., species can be absent from areas simply because they have been historically unable to reach them and it is quite possible that the range of environmental conditions wherein a species is now found may be rather narrower than their actual environmental tolerances.

4.2 The Search for Pattern

Understanding the multiple influences that contribute to species' distributions is a primary concern of both biogeography and macroecology, the explicit goals of which ‘boil down’ to:

1. The search for pattern in the distributions of (or of parts of) the global biota
2. The identification of the processes that generated those patterns, across diverse spatial and temporal scales

Which of these goals is ‘primary’ to understanding biogeographical pattern is a much debated question, though it seems to me that there is no escaping the fact that distribution *patterns* are a product of historical *processes* across a great diversity of time scales (McDowall 2004b, 2008). How these goals in biogeography are to be achieved has become highly controversial and ardently debated over the past 40 or so years, perhaps longer. Lawton (1996) cited MacArthur's (1972) comment that fundamental science is a “search for repeated patterns”, adding that a “key question in ecology ... is [determining] which local processes...scale up, and have a significant

influence on, patterns in species' distributions and ecosystem processes, across landscapes, biomes and the biosphere." With the addition of a time dimension, much the same can be said of biogeography. Wiens and O'Donoghue (2004), for instance, argue that "biogeographical patterns result from ecological processes that influence dispersal [or 'dispersion'] at different spatial and temporal scales." Ultimately, unless one is particularly interested in faunal regions or provinces (and some biogeographers are – Cockayne 1917; Dell 1962; Udvardy 1969; Briggs 1974; Cox 2001; Unmack 2001; Morrone 2002; Proches 2005; Merrick 2006; Greve et al. 2005), patterns become especially interesting when the processes that generated them are inferred or discovered.

According to Brown et al. (1996) "biogeography is about the structure and dynamics of geographic ranges", i.e., about changing spatial patterns, and the relationships between these ranges and the phylogenies of the taxa involved, about the processes that produced the patterns, and so about the history and ecology of biotic distributions. They drew a distinction between "dynamic processes of colonization and extinction (sometimes speciation)...[and] niche processes of mechanisms of limitation by environmental variables". But, as Brown et al. (1996) realised, historical and ecological processes operate simultaneously – they are, if you like, the warp and weft of the same fabric. They thought that "...often one or the other may be sufficient to explain a particular pattern..." but, in the end, the "...history of lineage is profoundly influenced by the history of place". Thus, when we examine and try to interpret contemporary biotic distributions we need to look at their roots in both history and ecology. Ultimately, much of biogeography is involved in distinguishing, and teasing apart, the relative roles of these two factors at both global and local scales (Hérault and Honnay 2005). An awareness of this history/ecology dichotomy seems to date back at least to the time of French biogeographer de Candolle (1820) (Nelson 1978).

4.3 Dispersal and the Question of History and Ecology

Endler (1982) emphasised the importance, as well as the difficulty, of addressing both historical and ecological questions in biogeography, and it is perhaps because of this difficulty that much of the biogeographical literature seems largely to ignore or proscribe one or other. Often the problem is that it is unclear whether, and which aspects of, observed patterns relate to history or which to ecology. There is, for some, a belief that history and ecology apply at different spatial and temporal scales. Gray (1989), for instance, a disciple of Croizat (see Croizat 1958, 1964), reckoned that: "Historical explanations have been used to explain regional patterns whereas ecological explanations have been used to explain more local patterns", and he contended that ecological arguments are opposed to historical explanations. However, this is no more than an assertion, which seems to me, at best, dubious, and I can find no reason to accept it. Ebach and Humphries (2003) partitioned biogeography on the basis that historical biogeography is relevant to macroevolution, but that (in their view) ecological biogeography applies to microevolution, conservation

and ecology, and that assertion, too, is highly debateable. Hengeveld and Hermerik (2002) sought to integrate ecology and biogeography but they, also, thought that the separation of history and ecology arises from addressing distributions at different spatial scales – implicitly regarding the effects of ecology as being a more local scale effect. Most recently, Wiens and O'Donoghue (2004), however, alluded to a “major chasm [that] now separates these research areas”, and they were concerned that “historical biogeography has divorced itself from biological questions that it might be uniquely qualified to answer”. Kodandaramaiah (2009: 327) concurred, asserting that “the two arms of biogeography, ecological and historical biogeography, are separated by a conceptual gap” and thought that “integration of them has been minimal, especially in the last few decades.” Wiens and O'Donoghue (2004) found that taxon-oriented phylogenetic studies generally do not set out to address the ecological processes that explain large-scale biogeographical patterns, and they further asserted that in general “large-scale biogeographical events are...the outcome of ecological processes, [so that] a dichotomy between historical and ecological processes is artificial”. I agree, entirely, and the present account seeks, in part, to address this false dichotomy (May 1986) at a medium-scale level: for the New Zealand freshwater fish fauna, across time and through space. Others have attempted to do the same for other scenarios, especially a recent paper by Filipe et al. (2009) on the biogeography of the freshwater fishes of the Iberian Peninsula. They thought (p. 2,097) that “The contrasting roles of history and the modern environment [= ecology] in structuring biotic assemblage...play important roles, but [that] it is difficult to tease apart their respective contributions”, but as I do in this book, Filipe et al. “expected the influence of barriers to dispersal to differ between species that are tolerant of salt water, if the latter use an additional dispersal pathway through the marine environment.”

Not all biogeographers attempt, in practice, to focus on the roles of both ecology and history. For some (Humphries and Parenti 1999; Craw et al. 1998; Ebach et al. 2003), the search for pattern relates primarily to earth history, and the focus is at the biota/community level rather than addressing individual species' patterns. Ebach et al. (2003), for example, asserted that the primary issues of biogeography are about area relationships, and that biogeography is not about finding individual species' histories (ancestor-descendent relationships and event-based scenarios)”, but this approach, which is biota-based, makes unwarranted assumptions that similar patterns have similar causes, and pays no attention to examining the validity of such assumptions. Knapp (2005) opined that “the [Croizatian] dictum [that earth and life evolve together] is self evident and true across all time scales”, but she gave no explanation or justification for that view. Again, it is sheer assertion, and I believe it to be false. There are plenty of instances where distribution patterns violate this principle. Gaston (2000) considered that “no single mechanism need adequately explain a given pattern, that observed patterns may vary with spatial scale, that processes at a regional scale influence patterns observed at local ones, and that no pattern is without variations and exceptions (see also Brooks and McLennan 2002).

The neglect, or rejection, of the role of ecology (and particularly dispersal) as a major driver of distribution patterns is especially prevalent among the panbiogeog-

raphers, and the vicariance and cladistic biogeographers. These historical biogeographers don't just ignore the role of ecology, but go far further and tend explicitly to reject a role for ecology, and also reject dispersal as influential in understanding historical biogeography – except, perhaps, where other approaches fail to generate what are viewed as consistent, congruent patterns (Croizat 1958, 1964; Croizat et al. 1974; Heads 1989; Craw et al. 1998; Humphries and Parenti 1999; Grehan 2001; Heads and Patrick 2003; Knapp 2005). It is almost as if only earth history is really important (Ebach et al. 2003), and that ecology (dispersal) should be allowed to intrude only when all else fails – a sort of tactic of last resort (Croizat et al. 1974; Santini and Winterbottom 2002; Brooks and McLennan 2002).

Wallis and Trewick (2009: 3,551) took the position that “The null hypothesis may be vicariance...[but]...If phylogenetic data make this assertion untenable, then alternative origins and mechanisms for dispersal should be sought.” However, Kodandaramaiah (2009: 329) recognised that dispersal and vicariance can generate the same patterns”, and to the extent that this is so, Wallis and Trewick's ‘null hypothesis’ is not a lot of help. Shepherd et al. (2009: 1,972) thought that “Numerous studies employing molecular systematics and molecular dating have ... demonstrated long distance dispersal in cases where the geological setting meant that a vicariant origin for the disjunction is possible.” Thus, when Rosen (1978) explicitly suggested that dispersal should be invoked only after a vicariance model has been falsified, and based this on his presumption that earth history is the primary driver of pattern, it seems, to me, to result in a biogeography that clearly falls far short of what can be observed even of contemporary dispersal processes, let alone that which is historical. It makes for a strange kind of science when some practitioners, like some of those mentioned above, can disavow the role of a process, whereas others are observing it, or are actually measuring its effects (Figuerola et al. 2005), or exploring its explicit role in biogeography (Beck and Kitching 2007). According to Lieberman (2003) “range expansion was treated as a significant process by ecological biogeographers only, whereas historical biogeographers viewed it as a kind of noise obscuring vicariance, the signal of interest,” and this seems, to me, a nonsensical approach. Sanmartin and Ronquist (2004) described vicariance and dispersal as “competing hypotheses” and they suggested that “Current methods of biogeography are based on the vicariant model because nearly any distribution pattern can be explained by dispersal, making dispersal hypotheses resilient to falsification.” It seems to me curious that a choice of method is made that favours an ability to falsify hypotheses in preference to a recognition of what actually happens, despite this sometimes being hard to authenticate or corroborate. Crisci and Katinas (2009) seek ways to integrate these divergent approaches, in contrast to debating them as binary opposites.

Some of this conceptual dichotomy is simply methodological, in general a rejection of a role for dispersal, at least in practice, even though vicariance and cladistic biogeographers often deny a rejection of a role for dispersal. In a thoughtful paper, Kodandaramaiah (2009: 329) explored several modern methods of biogeographical analysis and concluded that these methods inappropriately place too high a ‘cost’ on dispersal. He thought that parsimony methods have largely ignored...the vagility or

intrinsic dispersibility of a species” and that, for instance, Sanmartin and Ronquist’s (2004) DIVA program, uses costs that are heavily prejudiced against dispersal scenarios, irrespective of how vagile a taxon of interest is, and (p. 333) argued that “vagility should be explicitly taken into account in all historical biogeographical analyses.” He (p. 329) thought it unreasonable to assume...that amphibians, that are well-known for their intolerance to salinity have the same probability of colonising Madagascar from Africa as a migratory bird....Ideally, costs should be set based on the knowledge of the ecology of the organism.” He realised (p. 330), that “completely congruent area cladograms do not always translate to evidence for speciation driven solely by vicariance if the taxa in question have different vagility potential” and he explored the implications of giving various ‘costs’ to dispersal in analyses. He wrote (p. 331) of how “vicariance events have been invoked [in highly vagile butterflies] and even used to calibrate age estimates” and was critical of a “vicariance-centric assumption that ancestors were extremely widespread but their descendants not.” He (330) discussed the fact that butterflies, “being flying insects, are able to disperse longer distances and across marine barriers... [and that]... it is safe to assume that butterflies have a much higher probability of transoceanic dispersal than amphibians...the rigour of...biogeographical hypotheses hinges very little on the analytical method, but largely on the ecology and life history of their taxon.”

Croizat and his followers can, in my view, be accused of seriously under-rating the role of dispersal as a driver of biotic distribution patterns across vast spatio-temporal scales (McDowall 1978, 2002, 2004b, 2008). Some biogeographers have asserted that dispersal capabilities do not explain the geographical distributions of taxa, and that there is little relationship between means of dispersal and a species’ geographical distribution (Craw 1989; Michaux 1998; Heads and Patrick 2003), but I believe that assumption, too, is simply wrong. You don’t find these workers much exploring the biogeography of albatrosses or tunas – though Chin et al. (1991) did discuss the biogeography of a large, marine-shore brown alga (*Macrocystis*), which is spread around the entire cool Southern Hemisphere as well as occurring in coastal California, suggesting panbiogeographical explanations based on ancient earth history that seem, to me, plainly silly (see Coyer et al. 2001). Though, Craw (1989) has claimed to have “overwhelming evidence against the dispersal position”, he provided none. Moreover, he further argued that “Croizat’s extensive studies have shown the [dispersal position] to be wrong”, but again he was not explicit and provided no detail. He disputed Mayr’s (1982) view that organisms with different dispersal capabilities, such as earthworms and freshwater fish will have totally different distribution patterns from butterflies and birds” (see also Page 1989; Grehan 1989). He (Craw 1984) cited Croizat finding that “apparently highly vagile organisms like birds and butterflies exhibit very similar dispersal patterns to extremely sedentary organisms with no obvious means of dispersal, such as earthworms and flightless beetles”, and no doubt it is possible, with care, to find instances where this is true, but it is certainly not a generality, and if you, for example, compare albatrosses with onychophorans, or tunas with parastacid freshwater crayfishes and hydrellid mussels, there are often deep differences in pattern that look, at least to me, like a differential output of processes, like dispersal.

Sherman et al. (2008: 106), on the other hand, drew a contrast between “species with direct development and highly philopatric dispersal through to species with planktotrophic larvae that spend months in the water column and have the potential for passive dispersal over large distances.” For New Zealand, Wallis and Trewick (2009: 3,551) concluded that although for some taxa “it might be hard to find” overseas linkages for taxa “that we expect to be poor dispersers across oceans (ratites, frogs, freshwater linked fish) ... we should not be surprised to find overseas linkages for volant birds, mammals and insects, tough-seeded coastal plants ... and plants with wind dispersal mechanisms.” Moreover, there is a reasonable expectation that some distribution patterns driven by prevailing winds or ocean currents can lead to highly congruent distribution patterns across a diverse range of unrelated taxa (and see McGlone 2005), as Kodandaramaiah (2009) also clearly believes. So, the common patterns may have common causes that have nothing to do with earth history. McGlone (2006) drew explicit attention to the attributes of some plants, such as those with hooked or barbed seeds, sticky fruits, or exceedingly small spores or seeds, which make an unusually high proportion of non-endemic species spread widely across the globe.

Cladistic biogeographers such as Ebach et al. (2003) have postulated that “Tectonic theory reformed biogeography in so far that centres of origin and dispersal are no longer [even] relevant in explaining general patterns of taxic distribution” – an assertion that seems to me to be, at best, fundamentally flawed or, again, simply wrong (McDowall 2002, 2004b), even recognising that Ebach and Humphries (2003) are interested primarily in broad scale biotic/area relationships and prefer to view distributions on a broad-scale biotic/regional scale. They claim, that “the guardsman’s role in biogeography is to be vigilant as to what constitutes common sense in the ontology of biogeography rather than expounding narratives as explanations”, and this may be all very well, but in writing that they have simply shifted the debate from: “What is biogeography?” to: “What is common sense?” and, as is so often true, what one sees depends on where one is ‘looking’ from. From where Ebach and Humphries (2003) are ‘looking’, it seems that common sense requires analysis of broad scale patterns in what seems, to me, to be a ‘top-down approach to biogeography’, and in which there is no significant role for dispersal. From where I ‘look’, it is clear that dispersal has been a key element in assembling the biotas of many lands over geological time scales, especially in New Zealand (McDowall 1964, 2002, 2003, 2005, 2008) and, moreover, that individual species’ narratives can combine to tell a coherent story in which dispersal may sometimes play a major role – a ‘bottom-up’ approach: essentially, that the sum is the whole of its parts. Furthermore, if biological taxa do have common histories as regards place, should we not expect to find common patterns that will, as appropriate, accumulate in bottom-up fashion to form a general pattern consistent with geographical history? If all biogeography is a product of history, as Ebach and Humphries (2003) insist, is there anything to lose by addressing questions from both top down and bottom up analyses? I think not. I think there is far too much inadequately supported assertion relating to method, especially by the panbiogeographers and vicariance biogeographers. So, there has been vigorous debate in biogeography,

much of it methodological, with regard to both interpreting pattern and inferring process. It seems to me that to some extent the various schools of biogeography are simply “talking past each other” (Metge and Kinloch 1984). Some distributions almost certainly contain elements of both dispersal and vicariance and they probably cannot easily be teased apart. Resorting to explaining all pattern by Gondwanan vicariance does not seem, to me, to be the right approach.

There has been a pervasive historical problem that hypotheses generated to explain the distributions of a variety of southern taxa, whether based on the former existence of Gondwana or resulting from long-range, transoceanic dispersal and have proved in neither case falsifiable or testable, though the vicariance biogeographers and panbiogeographers would deny that for the discipline of their choice. Lack of testability has perhaps been especially true of dispersal – for which it has been suggested that ‘special pleading’ using dispersal is a major methodological issue (see especially Ball 1975, 1983). Those who have sought universal explanations in Gondwana have argued that this logical shortcoming is not true of vicariance hypotheses, on the grounds that the parallel distribution patterns in different groups of unrelated taxa provide mutual tests of validity. However, it does not necessarily follow that a vicariance explanation is the only one, or for that matter that congruent patterns have a common explanation (i.e., that common patterns have common causes: McDowall 1978). The meaning of this congruence remains controversial as it is possible to explain congruent patterns using various explanations, and sometimes different explanations for different components.

Controversy is especially true of the biotas of the southern lands formerly involved in Gondwana, as these lands are positioned around the cool/cold Southern Hemisphere in such a way that congruent or parallel patterns of distributions of taxa on these lands could result from *either* their former presence on Gondwana, *or* long-distance transoceanic dispersal around the Southern Ocean, *or*, in fact, even from some of both within the same or different taxonomic groups, i.e., there could well be an ancient distribution pattern influenced by an original presence on Gondwana, but then augmented, or overlaid, by more recent dispersal since Gondwana fragmented. Distinguishing these possibilities has proven difficult or even impossible. Hence tests from congruent patterns of distribution are potentially flawed, though panbiogeographers and vicariance biogeographers interested in southern biotas have been reluctant or unwilling to admit this.

Deliverance from these failings appears, to some, to have been provided by the use of molecular sequencing data. In part, this is because these data provide an ability to estimate the datings of the most recent gene flow between populations on the variously much-separated southern lands – put simply, this is the use of molecular clocks. And although these are to some extent controversial, and though there are difficulties calibrating them, they nevertheless at least provide indications of the relative timing of gene flow between various of the southern lands. In addition, patterns of phylogenetic relationship also provide a potential ability to discriminate monophyletic and non-monophyletic clades, and where monophyletic clades within a larger taxon are spread across southern lands in a pattern inconsistent with the distribution of these southern lands, it is possible to identify scenarios (paraphyletic taxonomic groups on single land

masses) that cannot have been simply a result of the fragmentation of Gondwana. Some biogeographers reject (disdain) molecular techniques, e.g., Ebach and Humphries (2003) simply dismiss molecular techniques as “insular and blinkered”, though they provide no coherent argument to explain their position. It just seems that they don’t much ‘like’ molecular approaches to phylogenetic and biogeographical analysis, a view that seems very much a minority one with little acceptance.

As a result of the use of molecular techniques, biogeography has entered a new age, with several things happening. Understanding of phylogenetic relationships has expanded greatly in both technique and taxonomic coverage. Hundreds of schemes exploring and explaining relationships are being published, month by month. When phylogenetic relationships are linked to geographic distributions, new insights are provided on how distribution patterns have been generated. An outcome of this has been that there has been a dramatic shift away from the scenario where dispersal has been largely dismissed or absolutely rejected as ‘unscientific’ and ‘untestable’, especially by panbiogeographers, and vicariance and cladistic biogeographers (Croizat et al. 1974; Ball 1975, 1983; McDowall 1978). However, this is no longer so true. It is, instead, being demonstrated, in case after case, that dispersal is highly likely, and dispersal has again become fashionable (de Queiroz 2005; Winkworth et al. 2005). Some of the postulated schemes of dispersal can only be described as astonishing, or even bizarre: e.g. the spread of the plant genus *Metrosideros* from New Zealand to Hawaii, an explanation that would be scorned were it not buttressed by molecular data. There are many other instances.

There have been additional processes happening. The histories of some oceanic islands have been examined and it is becoming increasingly recognised that many of them are relatively young, often volcanic, and that the only way that biotic elements could have reached them is by transoceanic dispersal – they have never been connected by emergent land from other lands. Hawaii, among all the oceanic islands of the world, is perhaps the clearest instance (Wagner and Funk 1995), but it is simply an extreme and more thoroughly known instance among numerous, highly-isolated, archipelagos of small, youthful, volcanic islands. There are many others, widely scattered around the oceans of the globe. In addition, some distinctly older, remote islands are being shown to have probably disappeared beneath the surface of the sea at some past time. This has been hypothesised, for instance, for the Chatham Islands, c. 800 km east of New Zealand (Campbell and Hutching 2007). They probably disappeared beneath the sea until c. 2–4 mya, or less. Again, some of the resulting, necessary, dispersal scenarios defy human imagination of the ability of biotic elements to disperse across substantial sea gaps – as is the case with the fauna of the Chathams including some now flightless insects (Trewick 2000). Even large, ostensibly continental islands like New Caledonia and New Zealand are suggested by some commentators to have, at times, been completely submerged beneath sea (Landis et al. 2008; Grandcolas et al. 2008), and the implication of such submergence is that the entire terrestrial biotas of these lands have arrived by dispersal across the sea. Hypothesised events of this sort are being corroborated by agreement between estimated times of submergence and estimates times of the dates of gene flow derived from molecular studies – as in the case of New Caledonia

(Grandcolas et al. 2008). Even if neither island/archipelago did completely submerge, there was certainly substantial immersion, and this would have led to substantial extinctions or bottlenecks. Evidence is being amassed that a large proportion of the faunas and floras of these large islands arrived there since such islands emerged, indicating substantial transoceanic dispersal (Winkworth et al. 2005). So, there is a major revolution going on in global biogeography, much of this driven by geological and molecular studies relating to the Southern Hemisphere lands formerly regarded as fragments of Gondwana (McGlone 2005; Trewick 2000; Trewick and Morgan-Richards 2005; Trewick et al. 2007; Wallis and Trewick 2009).

An interesting evolution of perspective on the origins of southern biotic elements relates to the distribution of a freshwater triclad platyhelminth *Dugesia*. Ball and Fernando (1969) recorded the genus *Dugesia* as occurring on all the lands formerly associated with Gondwana, as well as on remote Crozet Island in the sub-Antarctic. They argued, a priori, that *Dugesia* is incapable of dispersing across ocean gaps, and that its range must therefore be due to a former connection between Crozet and Gondwana. But Crozet is regarded as a relatively young, volcanic island, which would suggest the island was never connected to Gondwana, and that *Dugesia* must be capable of transoceanic dispersal. If that is so, then attributing its entire range on former Gondwana lands to their former Gondwanan connection is at least fraught (McDowall 1973).

Ball (1975) has argued eloquently for the need for biogeography to be based on hypotheses that can be test/falsified and, in the study environment of that time now more than 35 years ago, he could not envisage how dispersal hypotheses could be tested. This left biogeographers in a dilemma that one of the observed processes in contemporary biology – the continual arrival of propagules of species novel to an isolated land like New Zealand – provided only a limited prospect of being testable as a contributor to more ancient biogeographic analyses; according to Ball's criteria dispersal hypotheses are narratives, leaving dispersal biogeography with a limited conceptual foundation. But Ball was only partly right, as geological knowledge of some islands, like Crozet, suggests that, unless it can be decisively demonstrated that they were formerly connected to some other land area, biotic elements on such islands must have reached them by dispersal.

Thus, there is a major revolution going on in biogeography that is in a substantial sense reactionary to the purported panbiogeographic/vicariance/cladistic biogeographic revolution of the 1970s and 1980s (McGlone 2005). The practitioners of these approaches claimed the methodological 'high ground' on the basis that dispersal biogeography was a narrative approach to the field and unscientific. But it is not like that anymore. As just discussed both molecular techniques and geological knowledge are placing biogeographers in situations where dispersal can be evaluated and corroborated. Moreover, some of the biogeography of the 1970s was suggesting that biotic distributions proved that some lands must have once had land connections, leading to hypotheses that other biotic elements on these lands achieved their distributions through processes relating to land connections, and the arguments became decidedly circular (McDowall 1973). How things have changed, especially with the advent of molecular techniques, though there has been more to it than that.

4.4 Biogeography: 'Bottom Up' or 'Top Down'

Gaston and Blackburn (1999), in pointing to the need to address macroecological patterns at a series of spatial scales, allowed for a substantially 'bottom-up' approach. Their preoccupation with ecology rather than history is thus in marked contrast with panbiogeographers and vicariance/cladistic biogeographers, especially the likes of Ebach and Humphries who seem to espouse an entirely 'top-down' historical approach. Gaston (2000), for example, thought that "consideration of spatial variation in...the differences between entities rather than simply their numbers has been remarkably sparse."

In the present work I address distinctive life history strategies (ecology) and their implications for distribution and diversity, and consider that this has general applications for global patterns of biodiversity. Nonetheless, a dichotomy between ecological and historical approaches is another false dichotomy (May 1986). I firmly believe that dual approaches are needed (McDowall 1978, 2004b, 2008) and I seem to be far from alone in thinking that biogeography needs such duality. Wolf et al. (2001), for example, recognised that "an emerging problem is that taxon groups with the same area cladograms may still have had very different biogeographies" – raising the prospect that "rampant long distance dispersal [may have] obscured vicariance patterns", at least for fern taxa. Brownsey (2001) recognised an apparent enigma of an ancient group like ferns often seeming to have a relatively recent presence in New Zealand, and he attributed this to long distance dispersal. I doubt that this perspective would have emerged with a 'top-down' approach to explanations of patterns. Grandcolas et al. (2008) have made similar observations for New Caledonia. I think that vicariance biogeographers reject or ignore this at their peril.

A highly significant book Wagner and Funk (1995) explored the way Hawaiian biotic elements reached and dispersed across the archipelago as new islands emerged from the sea and others eroded and disappeared. Price and Wagner (2005), for example, asserted that the Hawaiian biota, as a whole, is entirely dispersal in origin. Cox (1998), McGlone et al. (2001), McGlone (2005), Gillespie (2002), Wright et al. (2000, 2001), Wilkinson (2003), Wanntorp and Wanntorp (2003), Cowie and Holland (2006) and Garb and Gillespie (2006) have all explored the role of dispersal in producing the biotas of oceanic islands, these, of course, being places where the role of dispersal can perhaps be isolated from other influences because some islands have never had any land connections and the origins of their biotas seem to derive wholly from dispersal processes. But there is no reason to suppose that what happens on continental masses is fundamentally different, in principle, from what happens on islands, even though the relative importance of historical and ecological influences may differ, and we are back with the dilemma of separating them. Denying the role of dispersal only obfuscates some of the biogeographical processes involved. Nevertheless, the panbiogeographers and cladistic/vicariance biogeographers would probably persist in arguing that patterns always reflect ancient land connections and vicariant processes, as Nelson (2006) has recently done for Hawaii (but unconvincingly – see Holland and Cowie 2006).

4.5 The Biogeographical Synthesis

Brown et al. (1996) saw “encouraging signs of the emergence of a synthetic (biogeographic/macroeological) perspective that incorporates information from phylogenetic reconstruction, the fossil record, and ecological studies, to provide a more complete understanding of the processes that have shaped geographical distributions”. They thought that “the apparent division between ‘ecological’ and ‘historical’ biogeography inhibits a thorough synthetic understanding of the patterns of distributions and the contemporary and historical processes that have produced them.” As they recognised, and as I noted above, the realities are that all history is influenced by ecology, and that all ecology has historical implications – they are ‘different sides of the same coin’. Gaston (2000) saw that patterns in biodiversity exhibited by taxa rest on contingencies (for example physical dispersibility, resource requirements, and evolutionary history), and so it is all complexly multi-layered, both spatially and temporally.

Part of the journey towards resolving and understanding the differences in approaches across the diversity of biogeography in my view derives from the contribution of molecular data and phylogeography (Avice 2000, 2009; Riddle 2009). To a considerable extent, the availability of molecular data (of which commentators, like Ball (1975) and others seeming to want more explicitly testable biogeographic hypotheses, were unaware), are providing the ability to discriminate between early vicariance processes and more recent dispersal processes, though there will always remain difficulties, as for instance in situations when dispersal processes took place not long after vicariance processes were no longer possible as a result of separations of land surfaces across which species could once have spread. I explicitly reject (as I suspect many others do – see Riddle 2009) the view of commentators like Ebach et al. (2003), that the use of molecular information is “insular and blinkered”. Rather, I think, with Zink et al. (2000), that molecular phylogenetic approaches “enrich biogeographical analysis”, especially insofar as they provide “a temporal perspective to add to the spatial perspective important to all biogeography”, but this seems of little interest to those interested only in pattern. It seems to me that data from phylogeography (Avice 2000, 2009) are increasingly helping to resolve some of these issues, and are providing the capacity to arbitrate between the roles of history and dispersal, by providing estimated ages of disjunct populations of species, or of sister taxa and relating these to known geological histories, as well as estimates of the earliest presence of species in geographical areas (Hurr et al. 1999; Winkworth et al. 1999, 2005; Avice 2000; Wright et al. 2000, 2001; Swenson and Hill 2001; Swenson et al. 2001; Knapp et al. 2007; Craw et al. 2008, and see Wallis and Trewick 2009 for a recent New Zealand-based synthesis). Thus, with the application of ‘molecular clocks’ no matter how inaccurate they may seem to be, we have an approach that is informative in helping to separate the roles of history and ecology in biogeography. Moreover, an understanding of lineage and phylogenetic relationships of taxa, whether from morphology or genetics, is also proving to be crucially important to clarifying distribution patterns,

including those of New Zealand's freshwater fishes (Waters et al. 2001a, b; Waters and McDowall 2005; Waters and Craw 2006), the subject of the present book.

Though a biogeographical synthesis of history and ecology is not simple to achieve, I think that biogeography avoids confronting this issue in biogeography at its peril. I reject the assertions by Craw (1989), Gray's (1989) and Grehan (1989) observation that in biogeography, ecological explanations are opposed to historical explanations as both wrong and unhelpful. Gray (1989) thought that "traditional explanations of distribution and abundance have been an uncomfortable mix of both ecological and historical explanations" – but it seems to me that if we are to confront the reality of what has happened in nature, through history and across space, how can they be anything else? As Crisci (2001) observed, "A solution for the ecology-history opposition is certainly needed. Ecology and history have played roles together at all times, [and] they are indissolubly tied together" (see also Crisci and Katinas 2009). I agree.

Though Zink et al. (2000) found that "few empirical studies document the relative role of vicariance and dispersal...they presented an attempt to do so for the bird fauna of the "aridlands of North America", by application of molecular phylogenies, thinking theirs to be "one of the first assessments of the relative roles of dispersal and vicariance" in shaping biodiversity, in their case in relation to a section of a continental bird fauna. Greve et al. (2005: 164) "note that whilst the importance of dispersal in ecology has never been disputed, its significance in historical biogeography has been the subject of long-standing debate", and they point to "mounting evidence of the importance of dispersal [that] cannot be ignored as a significant process affecting biogeographical patterns.... Whilst early vicariance may have set the board at the Southern Ocean ... the later game has clearly been one of dispersal."

Interestingly, Jackson et al. (2001) observed that "Because shoreline boundaries of lakes and rivers were perceived as limiting the potential for movements and dispersal by aquatic organisms, early ecologists focussed on the factors operating within each individual system in a more holistic manner than terrestrial ecologists, who placed more emphasis on dispersal and colonization to infer species' abundance and composition." However, Filipe et al.'s (2009: 2098) exploration of the distributions of fishes on the Iberian Peninsula, mentioned earlier, separates "groups of species with distinct tolerances of salinity to assess the effects of marine and terrestrial barriers on fish distributions" and (p. 2102) they concluded that "peripheral species [i.e. those with salinity tolerances] contributed most to the similarities within provinces" and (p. 2103) found that the "diminished role of river basin boundaries in determining the distributions of peripheral species ... is probably due to dispersal of fish along coastlines. Thus, although, normally, freshwater fishes are viewed as having very limited dispersal ability, as Filipe et al. show, this is not always so. Despite the pessimism of Craw (1989), Gray (1989) and Grehan (1989), that distribution patterns are not related to ecology (dispersal), in the New Zealand freshwater fish fauna they most certainly are, as this book goes on to describe.

References

- Avice JC (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA, 464 pp
- Avice JC (2009) Phylogeography: retrospect and prospect. *J Biogeogr* 36:3–15
- Ball IR (1975) The nature and formulation of biogeographical hypotheses. *Syst Zool* 24:407–430
- Ball IR (1983) Planarians, plurality, and biogeographic explanations. In: *Evolution, time and space*. Systematics Association Special Volume, pp 409–430
- Ball IR, Fernando CH (1969) Freshwater triclads (Platyhelminthes: Turbellaria) and continental drift. *Nature* 221:1143–1144
- Beck J, Kitching IJ (2007) Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Glob Ecol Biogeogr* 16:341–349
- Briggs JC (1974) *Marine zoogeography*. McGraw-Hill, New York
- Brooks DR, McLennan DA (2002) *The nature of diversity: an evolutionary voyage of discovery*. University of Chicago Press, Chicago, IL
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries and internal structure. *Ann Rev Ecol Syst* 27:597–623
- Brownsey PJ (2001) New Zealand's pteridophyte flora – plants of ancient lineage but recent arrival? *Brittonia* 53:284–303
- Campbell HL, Hutching G (2007) *In search of ancient New Zealand*. Penguin, Auckland, NZ, 238 pp
- Chin NKM, Brown MT, Heads MJ (1991) The biogeography of *Macrocystis* (Lessoniaceae). *Hydrobiologia* 215:1–11
- Cockayne L (1917) Notes on New Zealand floristic botany, including descriptions of new species. *Trans Proc N Z Inst* 49:56–65
- Cowie RH, Holland BS (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J Biogeogr* 33:193–198
- Cox CB (1998) From generalized tracks to ocean basins – how useful is panbiogeography. *J Biogeogr* 25:813–828
- Cox CB (2001) The biogeographical regions reconsidered. *J Biogeogr* 29:511–523
- Coyer JA, Smith GJ, Anderson RA (2001) Evolution of *Macrocystis* spp (Phaeophyceae) as determined by ITS1 and ITS2 sequences. *Phycology* 37:574–585
- Craw RC (1984) Panbiogeography: a progressive research program. *Syst Zool* 33:1–13
- Craw RC (1989) New Zealand biogeography: a panbiogeographic approach. *N Z J Zool* 16:527–547
- Craw R, Heads MJ, Grehan JR (1998) *Panbiogeography: tracking the history of life*. Oxford University Press, New York, NY, 229 pp
- Craw D, Burrige CP, Norris R, Waters JM (2008) Genetic ages for Quaternary topographic evolution: a new dating tool. *Geology* 36:19–22
- Crisci JV (2001) The voice of historical biogeography. *J Biogeogr* 28:157–168
- Crisci JV, Katinas L (2009) Darwin, historical biogeography, and the importance of overcoming binary opposites. *J Biogeogr* 36:1027–1032
- Croizat L (1958) *Panbiogeography – an introductory synthesis of zoogeography, phytogeography and geology: with notes on evolution, systematics, ecology and anthropology, etc.* Publ. Author, Caracas, Venezuela, 3 vols
- Croizat L (1964) *Space, time, form: the biological synthesis*. Publ. Author, Caracas, Venezuela, 881 pp
- Croizat L, Nelson GJ, Rosen DE (1974) Centers of origin and related concepts. *Syst Zool* 23:265–287
- de Candolle A (1820) *Geographie botanique*. Dictionnaire des Sciences. Strasbourg. Levrault 18:395–442

- de Queiroz A (2005) Resurrection of oceanic dispersal in historical biogeography. *Trends Ecol Evol* 20:68–73
- Dell RK (1962) New Zealand marine provinces: do they exist? *Tuatara* 10:43–52
- Ebach M, Humphries CJ (2003) Ontology of biogeography. *J Biogeogr* 30:959–962
- Ebach M, Humphries CJ, Williams DM (2003) Phylogenetic biogeography deconstructed. *J Biogeogr* 30:1285–1296
- Endler JA (1982) Problems in distinguishing historical from ecological factors in biogeography. *Am Zool* 22:441–452
- Figuerola J, Green AJ, Michot TC (2005) Invertebrate eggs can fly: evidence for waterfowl-mediated gene flow in aquatic invertebrates. *Am Nat* 165:274–280
- Filipe AF, Araujo MB, Doadrio I, Angermeier PL, Collares-Pereira MJ (2009) Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. *J Biogeogr* 36:2096–2110
- Garb JE, Gillespie RG (2006) Island hopping across the central Pacific: mitochondrial DNA detects sequential colonization of the Austral Islands by crab spiders (Araneae: Thomisidae). *J Biogeogr* 33:201–220
- Gaston KJ (2000) Global patterns of biodiversity. *Nature* 405:220–227
- Gaston KJ, Blackburn TM (1999) A critique for macroecology. *Oikos* 84:353–368
- Gillespie RB (2002) Biogeography of spiders on remote oceanic islands of the Pacific: archipelagos as stepping stones. *J Biogeogr* 29:655–662
- Grandcolas P, Murielle J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: a very old Darwinian island. *Phil Trans R Soc (Biol Sci)* 363:3309–3317
- Gray R (1989) Oppositions in panbiogeography: can the conflicts between selection, constraint, ecology and history be resolved. *N Z J Zool* 16:787–806
- Grehan JR (1989) New Zealand panbiogeography: past, present and future. *N Z J Zool* 16:513–525
- Grehan JR (2001) Panbiogeography and evolution of the Galapagos: integration of the biological and geological evidence. *Biol J Linn Soc* 74:267–287
- Greve M, Grammen NJM, Gaston KJ, Chown SL (2005) Nestedness of Southern Ocean biotas: ecological perspectives on a biogeographical conundrum. *J Biogeogr* 32:155–168
- Heads MJ (1989) Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *N Z J Zool* 16:549–585
- Heads M, Patrick B (2003) Biogeography. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. Otago University Press, Dunedin, NZ, pp 89–100
- Hengeveld R, Hermerik L (2002) Dispersal and biogeography. In: Bullock JM, Edward RE, Hails RS (eds) *Dispersal Ecology*. Blackwell, Oxford, pp 303–324
- Héroult B, Honnay O (2005) The relative importance of local, regional and historical factors in determining the distribution of plants in fragmented riverine forests: an emergent group approach. *J Biogeogr* 32:2069–2081
- Holland BS, Cowie RH (2006) Dispersal and vicariance in Hawaii: submarine slumping does not create deep inter-island channels. *J Biogeogr* 33:2155
- Humphries CJ, Parenti LR (1999) *Cladistic biogeography: interpreting patterns of animal and plant distributions*, 2nd edn. Oxford University Press, Oxford, 187 pp
- Hurr KA, Lockhart PJ, Heenan PB, Penny D (1999) Evidence for the recent dispersal of *Sophora* (Leguminosae) around the Southern Oceans: molecular data. *J Biogeogr* 26:565–577
- Jackson DA, Peres-Neto PR, Olden JD (2001) What controls who is where in freshwater fish communities - the roles of biotic, abiotic and spatial factors. *Can J Fish Aquat Sci* 58:157–170
- Knapp S (2005) Biogeography: space, form and time. *J Biogeogr* 32:3–4
- Knapp M, Mudaliar R, Havell D, Wagstaff SJ, Lockhart PJ (2007) The drowning of New Zealand and the problem of *Agathis*. *Syst Biol* 56:862–870

- Kodandaramaiah U (2009) Vagility: the neglected component in historical biogeography. *Evol Biol* 36:327–335
- Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA (2008) The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 143:173–197
- Lawton JH (1996) Patterns in ecology. *Oikos* 75:145–147
- Lieberman DS (2003) Paleobiogeography: the relevance of fossils to biogeography. *Ann Rev Ecol Syst* 34:51–69
- MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Harper and Row, New York, 269 pp
- May RM (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology* 67:1115–1126
- Mayr E (1982) The growth of biological thought. Belknap, Cambridge, MA, 797 pp
- McDowall RM (1964) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1973) Zoogeography and taxonomy. *Tuatara* 20:88–96
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2003) Hawaiian biogeography and the islands' freshwater fish fauna. *J Biogeogr* 30:703–710
- McDowall RM (2004a) Ancestry and amphidromy in island freshwater fish faunas. *Fish Fisher* 5:75–85
- McDowall RM (2004b) What biogeography is: a place for process. *J Biogeogr* 31:345–351
- McDowall RM (2005) Biogeography of the Falkland Islands: converging trajectories in the South Atlantic. *J Biogeogr* 32:49–62
- McDowall RM (2008) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McGlone MS (2005) Goodbye Gondwana. *J Biogeogr* 32:739–740
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of the biota. In: Allen RB, Lee WG (eds) *Biological invasions in New Zealand*. Springer, Berlin, Germany, pp 17–32
- McGlone MS, Duncan RP, Heenan PB (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J Biogeogr* 28:199–216
- Merrick JR (2006) Australasian freshwater fish faunas: diversity, interrelationships, radiations and conservation. In: Merrick JR, Archer M, Hickey G, Lee MSY (eds) *Evolution and biogeography of Australasian vertebrates*. Auscupubs, Oatlands, NSW, pp 195–224
- Metge J, Kinloch P (1984) Talking past each other: problems of cross-cultural communication. Victoria University Press, Wellington, N Z, 60 pp
- Michaux B (1998) Terrestrial birds of the Indo-Pacific. In: Hall R, Holloway JD (eds) *Biogeography and geological evolution of SE Asia*. Backhuys, Leiden, The Netherlands, pp 361–392
- Morrone JJ (2002) Biogeographical regions under track and cladistic scrutiny. *J Biogeogr* 29:149–152
- Nelson GJ (1978) From Candolle to Croizat: comments on the history of biogeography. *J Hist Biol* 11:269–305
- Nelson GJ (2006) Hawaiian vicariance. *J Biogeogr* 33:2154–2156
- Page RDM (1989) New Zealand and the new biogeography. *N Z J Zool* 16:471–484
- Price JP, Wagner WL (2005) Speciation in Hawaiian angiosperm lineages: cause, consequence and mode. *Evolution* 58:2185–2200
- Proches S (2005) The world's biogeographical regions: cluster analysis based on bat distributions. *J Biogeogr* 32:607–614
- Riddle BR (2009) What is modern biogeography without phylogeography? *J Biogeogr* 36:1–2
- Rosen DE (1978) Vicariant patterns and historical explanation in biogeography. *Syst Zool* 24:431–464

- Sanmartin I, Ronquist F (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Syst Biol* 53:216–243
- Santini F, Winterbottom R (2002) Historical biogeography of Indo-western Pacific coral reef biota: Is the Indonesian region a centre of origin? *J Biogeogr* 29:189–205
- Shepherd LD, de Lange PJ, Perrie LR (2009) Multiple colonizations of a remote oceanic archipelago by one species: how common is long-distance dispersal? *J Biogeogr* 36:1972–1977
- Sherman CDH, Hunt A, Ayre DJ (2008) Is life history a barrier to dispersal along an oceanographically complex coast? *Biol J Linn Soc* 95:106–116
- Swenson U, Hill RS (2001) Most parsimonious areagrams versus fossils: the case of *Nothofagus* (Nothofagaceae). *Aust J Bot* 49:367–376
- Swenson U, Hill RS, McLoughlin S (2001) Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. *Taxon* 50:1025–1041
- Trewick SA (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insects on the Chatham Islands, New Zealand. *J Biogeogr* 27:1189–1200
- Trewick SA, Morgan-Richards M (2005) After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostostomatidae). *J Biogeogr* 32:295–309
- Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Udvardy MDF (1969) Dynamic zoogeography, with special reference to land animals. van Nostrand/Reinhold, New York, 445 pp
- Unmack PJ (2001) Biogeography of Australian freshwater fishes. *J Biogeogr* 28:1053–1089
- Wagner WL, Funk VA (eds) (1995) Hawaiian biogeography: evolution on a hot-spot archipelago. Smithsonian Institution Press, Washington, DC, 467 pp
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Wanntorp L, Wannorp HE (2003) The biogeography of *Gunnera* L.: vicariance and dispersal. *J Biogeogr* 30:979–987
- Waters JM, Craw D (2006) Goodbye Gondwana: New Zealand biogeography, geology and the problem of circularity. *Syst Biol* 55:351–356
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, Esa YB, Wallis GP (2001a) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298
- Waters JM, Craw D, Youngson JH, Wallis GP (2001b) Genes meet geology: fish phylogeographic pattern reflects ancient rather than modern drainage patterns. *Evolution* 55:1844–1855
- Wiens JJ, O'Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19:640–644
- Wilkinson DM (2003) Dispersal, cladistics and the nature of biogeography. *J Biogeogr* 30:1779–1780
- Winkworth RC, Robertson AW, Ehrendorfer F, Lockhart PJ (1999) The importance of dispersal and recent speciation in the flora of New Zealand. *J Biogeogr* 26:1323–1325
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Divers Evol* 8:237–247
- Wolf GP, Schneider H, Ranker TA (2001) Geographic distribution of homosporous ferns: does dispersal disguise evidence of vicariance? *J Biogeogr* 28:263–270
- Wright SD, Yong CG, Dawson JW, Whittaker DJ, Gardner RC (2000) Riding the ice age El Nino: Pacific biogeography and evolution of *Metrosideros* subg *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proc Natl Acad Sci USA* 97:418–4123
- Wright SD, Yong CG, Dawson JW, Whittaker DJ, Gardner RC (2001) Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS+ETS). *J Biogeogr* 28:769–774
- Zink RM, Blackwell-Rojo RC, Ronquist F (2000) The shifting roles of dispersal and vicariance in biogeography. *Proc R Soc Lond B Biol Sci* 267:497–503

Chapter 5

Some Essentials of Freshwater Fish Biogeography, Fish Life Histories, and the Place of Diadromy

Abstract The biogeography of freshwater fishes is profoundly affected by the way freshwater habitats are highly fragmented into what could be called elongate islands (rivers). About half the New Zealand freshwater fish species are diadromous, diadromy being a dominating influence on the distribution of the species. Recognition of this prevalence of diadromy has influenced attitudes towards the origins and distributions of the freshwater fish species. The ability of diadromous species to reach an isolated archipelago like New Zealand, and to facilitate dispersal of species through coastal seas around New Zealand, has shaped the composition and biogeography of the fauna. A few species are derived from sister taxa in the seas around New Zealand. Much of the local diversification has resulted from the loss of diadromous migrations and the evolution of species with narrow ranges, that are confined to New Zealand fresh waters.

Keywords Diadromy • Dispersal • Evolution • Landlocking • Marine derivations • Speciation

5.1 Freshwater Fish Biogeography

The biogeography of freshwater fishes has some distinctive features. There is an enduring and widespread assumption that the ability of ‘freshwater fish’ to disperse between isolated water bodies is restricted, something that was well recognised by Darwin (1873: 343), who discussed how “lakes and streams are separated from each other by barriers of land.” The significance of oceanic barriers to freshwater fish migration continues to be well recognised (Lucas and Baras 2001; Helfman et al. 1997; Filipe et al. 2009).

Populations of freshwater fish species tend to be highly fragmented, and this is simply an explicit outcome of the discontinuous, highly fragmented, nature of the freshwater habitats in which fish live. Rivers and lakes tend to be highly isolated, physically, and, in the case of rivers, at least, to comprise elongated, narrow, flowing channels that form upstream/downstream patterns of hierarchical connectedness, with the upstream smallest streams joining to form progressively larger and larger waterways, and lakes often participating in these hierarchical connections, though sometimes being

entirely isolated. Freshwater fish species tend to form multiple metapopulations in the fragmented habitats they occupy. This is simply because, to move between separate waterways, fish must either cross land (which is generally impossible), move through the sea between one waterway and another (possible only for those that can osmoregulate at sea), or capitalise on rarely changing patterns of connectedness between freshwater bodies as a result of geological/hydrographic changes (as discussed for New Zealand's Southern Alps by Waters and Wallis 2000; Burridge et al. 2006; Waters et al. 2006 and Craw et al. 2008) These changes can include:

1. Headwater captures
2. Rivers wandering across flood plains, disconnecting and reconnecting as they do; and
3. May result from formation of downstream confluences between hitherto separate river systems, that are produced by extended coastlines during periods of lowered sea levels

5.2 Upstream/Downstream Trends in Riverine Ecology and Biogeography

In addition to the highly fragmented metapopulations of their fish faunas, especially from an ecological perspective, river systems have upstream-downstream trends or vectors that are substantially a consequence of a number of metrics – upstream-downstream shift in elevation and therefore ambient temperatures, increase in flow volume as a river accumulates the flows of its many tributaries, often changes in channel gradient, flow velocities, and substrate coarseness, with less steep gradients, slower flow velocities and finer substrates at lower elevations, and so there are often parallel changes in numerous features of the biological communities that depend on these various river channel attributes, including riparian vegetation and the land/water connection. These inter-related metrics are codified in the River Continuum Concept (RCC) (Vannote et al. 1980), and though the drivers of these changes are typically viewed as upstream/downstream vectors that relate to size and flow volume, nutrients and other variables that have impacts on fish communities, some of the gradients and changes may also have downstream/upstream vectors driven by the fact that, for some species, occupation of river systems is a result of upstream migrations of diadromous fishes that originate in the sea (Pringle 1997; McDowall 1988, 1998b). All of these trends have important biogeographical implications.

5.3 Questions Relating to Distribution, Dispersal and Salinity Tolerances

Despite the perceived restrictions of freshwater fishes to freshwater habitats, Darwin (1873) long ago recognised that some of the notable features in the distributions of freshwater fishes were the result of transoceanic dispersals of

marine tolerant life stages. And, over the past century or more, there has been the development of a series of groupings of freshwater fishes that aim to draw together fish taxa with different tolerances of increased water salinities.

British ichthyologist Boulenger (1905) listed four categories:

- (i) Those freshwater fishes that live part of the time in the sea, and this category he subdivided into anadromous fishes that breed in fresh water and catadromous fishes that breed in salt water.
- (ii) Those fishes living normally in the sea, but of which certain colonies have become restricted to fresh water (often landlocked in lakes), or which have separated themselves from the marine stock still represented on the neighbouring coast.
- (iii) Those fishes that, although entirely confined to fresh waters have as nearest allies species living in the sea, and which there is reason to regard as more or less derived from marine forms.
- (iv) Those fishes belonging to families entirely or chiefly restricted to fresh water.

In addressing these issues we must remember that while groups, usually specified at the family level, may be assigned to one of the above categories or another, there are likely to be included related taxa at a lower taxonomic scale (genera, species), that are exceptions to the general classification.

American ichthyologist J.T. Nichols (1928) presented another ecological classification of freshwater fishes, in which he drew a distinction between:

- (i) Continental freshwater fishes, dominated by the ‘carp-characin-catfish group’ (i.e., the group now known as the Ostariophysi – Nelson 2006), which he regarded as being very much restricted to fresh water, though there are sometimes very occasional euryhaline species among them.
- (ii) Peripheral freshwater fishes, a group that is regarded as being made up of elements with better-marked affinities to salt-water groups.

Then, in a series of papers, American ichthyologist George Myers (1938, 1949a, b, 1951) explored the question of salinity tolerances across the diversity of freshwater fishes, and he did so in some detail. Myers (1938) recognised that fish groups differ in their ability to survive in marine salinities. He showed that some fishes, and in fact including the largest taxonomic group, again the so-called Ostariophysi (carps, characins, catfishes and relatives), have very restricted ability to survive in salinities elevated above those found in typical running waters. These fishes, and a diversity of other, rather smaller groups, he referred to as ‘primary freshwater fishes’. Other groups of fishes, however, exhibit rather greater salt tolerance, and these he classed as ‘secondary’ freshwater fishes. These ideas (Myers 1951) culminated in a detailed review of the question, in which he concluded that fishes of fresh waters “may be classified...in the following groups”, which I summarise generally without listing the taxa that Myers included in each:

- (i) Primary freshwater fishes that are strictly intolerant of salt sea water. There are a few exceptions [in the listed families]...but they are exceedingly few.

- (ii) Secondary freshwater fishes that are rather strictly confined to fresh water but evidently capable of occasionally crossing narrow sea barriers; tolerance of sea water for short periods is known for many.
- (iii) Diadromous freshwater fishes that regularly migrate between fresh and salt water (in both directions) at definite period of their life cycle.
- (iv) Vicarious that are presumably non-diadromous freshwater representatives of partly or primarily marine groups.
- (v) Complementary freshwater fishes, often or usually diadromous and belonging to marine groups that become dominant in fresh water only in the paucity or absence of primary, secondary and probably also vicarious freshwater faunas.
- (vi) Sporadic fishes, being those that live and breed indefinitely in salt or fresh water, or which enter fresh water only sporadically and not as a part of a true migration.

Darlington (1957: 41) substantially simplified (and I think clarified) Myers' (1938, 1949a, b, 1951) scheme, listing only three categories of freshwater fishes:

- (i) A "primary division" including those "that are strictly confined to fresh water"
- (ii) A "secondary division" for those that "live chiefly in fresh water but have a little (not too much) salt tolerance"

and Darlington added to these:

- (iii) A "peripheral division" for "fishes that occur in fresh water but have much salt tolerance"

Darlington's categories have since been widely used. He derived the term peripheral from Nichols (1928: 6), who had referred to peripheral freshwater fishes being "made up of elements with better-marked affinities to salt-water groups", the species making up this group occupying "a vague northern circumpolar area (trouts and pikes); the southern tips of South America and Africa (*Galaxias*); Australia and the islands of the world in general". It needs to be understood that these terms (like so many similar sorts of biological categories) are not exclusive or precisely bounded, but that they form a broad continuum, with several peaks of abundance/species diversity at several points along that continuum.

In general, the application of the terms primary, secondary and peripheral, is usually at the taxonomic family level, i.e., all species within a family tend to fall into, or are regarded as falling into one of the three classes of salt tolerance, but even at that scale, there is sometimes quite wide variation within some families. Occasional species within 'primary' families may exhibit substantial salinity tolerances, and this may reflect a situation where the fish have been long exposed to elevated salinities, such as some cyprinids that live in the Caspian and Black Seas of eastern Europe, or the Baltic Sea in Scandinavia. Moreover, in 'peripheral' families some, or even many, of the species do not have, or are not regarded as having, high salt tolerances, largely because such species have a long history of no exposure to sea water, but typically species that were long ago derived from a diadromous ancestry in which there was such tolerance. Furthermore, in some of Darlington's 'peripheral' families, the ability to cope with elevated salinities may be restricted to a quite narrow, physiologically-mediated period of tolerance, and

may not be present throughout a fish's entire life (Fontaine 1975). Physiological tolerances may develop only at the life history stage that customarily shifts between biomes, perhaps best known in the so-called 'smolting' of juvenile anadromous salmonids prior to migrating to sea (and when they become silvery and develop the physiological ability to live in sea water). So, in addition to the 'peripheral' category not being explicitly bounded, there are also some additional intraspecific, temporal/life stage complexities, though the grouping has wide acceptance among fish biologists.

5.4 The Biogeographical Response

One of the explicit points of Myers' (1951) groupings was that in his view "Diadromous, complementary and sporadic fresh-water fishes seldom are of any particular importance in showing terrestrial geographical relationships", his point seemingly being that he considered such fishes to have the capacity to move between separate freshwater bodies, crossing marine barriers by passage through the sea, and so they were not informative, or at least not *as* informative, of biogeographical connections.

Boulenger (1902, 1905), for instance, had long before concluded that his groups (i) and (ii) listed above should be disregarded when dealing with the distributions and biogeography of fresh-water fishes. He argued that their geographical ranges are not regulated by the sea because they can migrate, or disperse through it, and he concluded that they must be dealt with in conjunction with marine littoral forms. Moreover, he thought that his third category was also of only secondary interest in the history of the fresh-water fauna. Of particular, present relevance, he did, however, recognise the likelihood that the genus *Galaxias* might be controversial and give rise to discussion, and he was so correct (see Chapter 8)!

But, as just noted, it was American ichthyologist George Myers (1938) who most explicitly subdivided freshwater fishes into groups based on their tolerance of marine salinities, and he drew attention to their biogeographical significance. His "primary" freshwater fishes, he later defined in biogeographical terms as "rigidly and only with unimportant exceptions confined to the freshwaters of continents and of islands which we know to have been connected with the continents during the Cenozoic", whereas the species in his "secondary" group are found "on many islands the continental connections of which are either dubious or known not to have existed during the Cenozoic" (Myers 1949b: 317). The modern view of such land connections may very different from what it was in Myers' time. As Darlington (1957: 41) put it, these groups defined by salinity tolerances are complex and cut across taxonomic lines. Moreover, the boundaries between those fishes "confined to fresh water", those with "a little salt tolerance" and those exhibiting "much salt tolerance" are highly subjective and inexplicit.

In the context of the present book, it is important, at the outset, to recognise that at the family level all of the freshwater fishes known to occur naturally in

New Zealand fall into Darlington's 'peripheral' category. Moreover, all of the families of fishes found in New Zealand fresh waters also include at least some species that Myers (1949a) would have classed (or did class) as diadromous, i.e. they customarily spend a part of the life cycle of each individual fish, in the sea, and there are regularly-timed migrations from fresh water to the sea and the reverse (both of which are, of course, necessary to complete the fish's life cycle). Thus, when exploring the biogeography of the New Zealand freshwater fish fauna it must be always remembered that there is a strong potential tendency for these fishes to have high ability to tolerate marine salinities.

However, just because all of New Zealand's freshwater fishes belong to *families* that are classed as peripheral, this does not mean that all of them have high tolerance of saline waters, or that those that can tolerate salinity can do so at all life stages: some of them probably don't, but it is probably reasonable to assume that they are derived from or closely related to groups that do have such high tolerance. In fact, *some* member species in *all* families represented in the New Zealand fauna are diadromous, and in *most* families *all* of them are, and so they undertake regular migrations between marine and freshwater biomes at regular, predictable life-history stages, and as a part of their normal life histories (McDowall 1964, 1988, 1990, 1995, 2002b).

5.5 The Question of a Marine Ancestry of Diadromous Fresh Water Fishes

It is of some interest to draw together here, and comment on, repeated suggestions that freshwater fishes regarded as having an ability to live in both freshwater and marine salinities are derived from a marine ancestry. Thus, Myers (1951: 12) considered that his 'vicarious' group appeared to be of "relatively recent derivation from marine types."

Statements of this sort have long been highly pervasive in the fish/biogeographic literature, and I think they are consistently untrue. Interestingly, Boulenger (1905) listed *Galaxias* among groups that had a marine ancestry. Regan (1905) recognised that at least some galaxiids spent time at sea, and he summarised that "The Galaxiidae present many analogies to the Salmonidae of the Northern Hemisphere, both being circumpolar groups of marine origin which are establishing themselves in fresh water. In both families we meet with non-migratory forms which appear to have finally left the sea..." He did not explain why he thought they had such a marine origin, or what he meant by "establishing themselves in fresh water", a viewpoint that has had a very long history in the literature on the Salmonidae (McDowall 2002a). While it might be that somewhere in the deep ancestry of some of these diadromous fishes there was a marine ancestor, the question is certainly controversial and a rigorous answer is probably inaccessible to discovery. The particulars of this debate aside, it seems to me highly likely that the joint ancestors of a diverse range of lower euteleostean fishes were diadromous and so that there was diadromy deep in the ancestry of the salmonids, themselves.

But this idea of a marine ancestry for some fish groups has long persisted, especially for many of the fishes found in the streams of remote islands. British stream ecologist Hynes (1970), for instance, stated that the freshwater fish faunas of Australia and New Zealand consist of "... recently acquired species of marine origins". The Australians Serventy and Raymond (1980) told of a "strong possibility that the ancestors of [Australian freshwater galaxioid] fish may originally have been a sea fish with a wide range over the Southern Ocean which later evolved into freshwater forms." Hawaiian marine ecologist Kinzie (1988) generalised that "Much of the freshwater biota on high Pacific islands is derived from marine ancestors. Traces of this marine origin are seen in the amphidromous life history patterns of these species", and he alluded to gobiid fishes. Radtke and Kinzie (1991) thought that "The gobioid fishes [of Hawaii]...though marine in origin, have invaded brackish and fresh waters probably several times." Loope and Mueller-Dombois (1989) considered that Hawaii's freshwater fish are "freshwater-tolerant fish derived from ancestors that spent their entire life cycles in the sea..." American ichthyologist Burgess (1989) wrote that "Invading marine species constitute an important component of the ichthyofauna....Many marine species spend at least a portion of their lives, often as juveniles, in the brackish lower reaches of insular rivers" and he mentioned eleotrids and sicydiine gobies. A British naturalist with an interest in the Falkland Islands fish fauna, Peter Lapsley (1993) suggested that "The distribution of *Lovettia* (Tasmania) (Fig. 5.1) and *Aplochiton* (Patagonia) (Fig. 5.2) [f. Galaxiidae] raises an interesting question as to whether their distant ancestors may not have been a single marine species which migrated into rivers, rather than

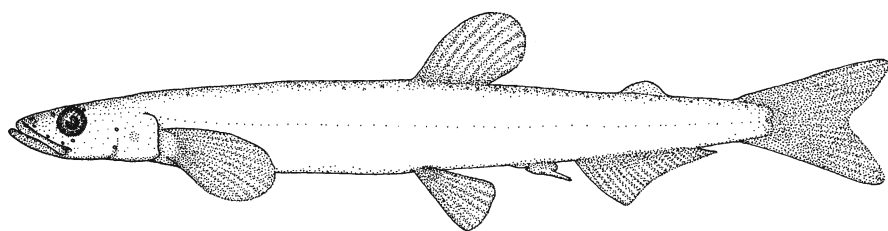


Fig. 5.1 *Lovettia sealii* the Tasmanian whitebait, 55 mm LCF (family Galaxiidae)

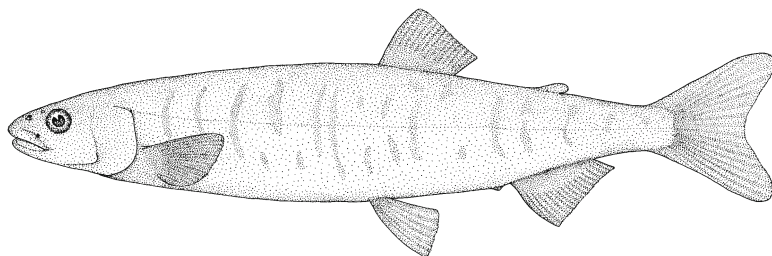


Fig. 5.2 *Aplochiton zebra*, 284 mm LCF (family Galaxiidae) the Patagonian puye or zebra trout

a freshwater species which went to sea and then crossed the vast tract of ocean.” Roumanian biogeographer Petru Bănarescu (1995) stated that: “Lineages of marine origin are more frequent in ...continental islands where primary freshwater animals are not numerous (Australia, New Zealand, New Caledonia, Madagascar), in islands even of continental origin which have been isolated from the mainland for long periods (the Antilles), or which have never belonged to continents (Indonesia, Polynesia, etc.). Americans Resh and Szalay (1995) concluded that “Most of the faunas of island streams, especially larger forms, are of marine origin. These include...all non-introduced fish,” while Sax et al. (2002) argued that “...most freshwater fish on islands originated as marine species that secondarily invaded the freshwater environment, including the five freshwater fishes that are native to Hawaii...” So the idea of a marine ancestry is widely pervasive in workers from diverse origins and with diverse interests.

Attribution of a marine ancestry has also applied in New Zealand, just as it has elsewhere. Fisheries Biologist Radway Allen (1956: 3) saw that the fact that “New Zealand [is] separated by nearly 2,000 mi. of sea presents peculiar difficulties for the establishment of freshwater fish. Hard though it is for terrestrial animals to cross an ocean barrier, it is still harder for freshwater fish; even such convenient devices as floating logs and birds’ feet are useless to him, and he is left with the waterspout and other violent atmospheric phenomena as almost his only resource.... Until the coming of man the only source available was the sea surrounding its shores and it is from this that our native freshwater fish seem to have come”, Allen concluding (p. 4) that “... their supposed marine ancestors no longer survive.” He concluded that the objections to an hypothesis of marine derivation were “... far slighter than those encountered by any other hypothesis”, such as “the existence of an extensive Antarctic land-mass to which all the southern continents and New Zealand were at one time joined, probably in the Tertiary ...”, though he somewhat surprisingly did not envisage a significant role for marine migratory, diadromous species, despite being aware of some of them. Tony Eldon (1992) was another, who wrote, of New Zealand’s freshwater fishes, that: “Many species and all the families have close links with the sea, from whence most of the families – possibly all of them – originated.” And palaeontologists Holdaway and Worthy (2006: 216) wrote of an “the overwhelming majority of species that invaded from marine environments during the Tertiary.” Unless these authors intended to convey the prospect that freshwater fishes moved through marine environments into New Zealand freshwaters, and that does not seem to be what they intended, then they are all largely incorrect. None of the above authors placed their assertions in a phylogenetic context. We need to distinguish very carefully between an origin in the sea and dispersal through the sea.

Mention of marine ancestry for freshwater fishes is thus highly pervasive, but a critical reading of the papers that these quotes originate from shows that although there *are* instances in which freshwater species are derived from a recent/close marine ancestry, far more often they are referring to species whose ancestries are among wider groups of diadromous (amphidromous) fishes (McDowall 2004), and they do not have a marine origin.

Such issues are of particular relevance to the biogeography of freshwater fishes, generally, and of special present relevance to those of New Zealand. It seems clear that two New Zealand species, the torrentfish and the black flounder, *are* species that have a local derivation from fishes that are found in New Zealand coastal seas (the torrentfish is related to the marine blue cod, *Parapercis colias* and the flounder to other species of *Rhombosolea* in coastal New Zealand seas). All of the others, however, appear to have a deep ancestry among other diadromous fishes and do not have any clear recent, or usually even longer-term, marine ancestry. This is an important distinction if we are to understand the historical/ecological biogeography of these fishes. Amateur New Zealand ichthyologist Gerald Stokell was among those who wrestled with this question, but he did so in ignorance of the extent to which the country's fauna is diadromous – he seems to have been aware of diadromy in relatively few New Zealand species. In the end, however, he could find no satisfaction in hypotheses that focussed on the likelihood that broad distributions of freshwater fishes around the lands of the Southern Ocean had a common marine ancestry (Stokell 1950, 1953). Beddard (1895) had long before reached the same conclusion, at least for the very widespread *Gl. maculatus* (Fig. 5.3) (which he referred to as *Gl. attenuatus*). Clearly, there are profound problems that derive from the proposal that freshwater fishes in very diverse and widely separated lands are derived from some equally widespread marine species that somehow afterwards disappeared from marine habitats in all of the various, widely separated areas where they once ostensibly occurred – it has to be nonsense. There is no doubt that most of those who made such claims of a marine ancestry had really not thought through the implications of such ideas with any care!

In general, it seems to me that a conclusion that particular freshwater fish groups, whether local or of widespread range, have a common marine ancestry is at best unhelpful, is rarely proven, is usually wrong, and is of only fleeting interest to biogeographers. The key biogeographical element is their ability to cope with prolonged life in the sea. This is another matter, altogether, the difference is perhaps subtle, but it is real, and it is also important.

One of the fundamental issues explored in this book relates to the implications for biogeography of varying life history strategies (= ecology). And, while there may be something of a conceptual and methodological dichotomy between broad

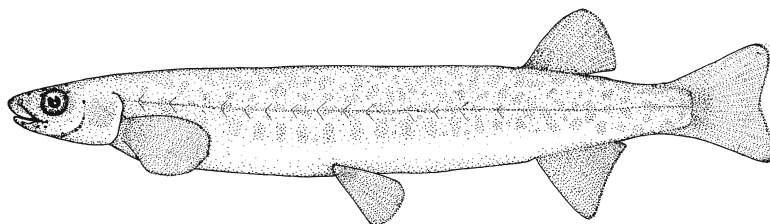


Fig. 5.3 *Galaxias maculatus*, 94 mm LCF (family Galaxiidae): perhaps the most widely dispersed known species of freshwater fish, known from Australia, Lord Howe Island, New Zealand, the Chatham Islands, Patagonian South America and the Falkland Islands (see fig. 7.2)

scale/historical patterns and local scale/ecological patterns, the present account reveals instances where *ecology* can influence distribution patterns over much broader spatial scales than does *history* (as discussed in Chapter 4: A conceptual basis for biogeography), and I show here that, in practice, some freshwater fishes can have essentially different distribution patterns from other freshwater fishes, and that these differences are structured explicitly around life history strategies, related dispersal abilities, and thus ecology, i.e. historical biogeography is to a considerable extent mediated by ecology.

The biogeography of New Zealand's freshwater fish fauna, with its deep life history dichotomy between diadromous and non-diadromous species, provides an important opportunity to achieve some partition of the roles of ecology and history in biogeography, and it is one of the purposes of the present book to do so.

In the decades since the propositions of Myers and Darlington in the mid-twentieth century, biogeographers have responded in variable fashion to understanding the biogeographical implications of the distributions of these diverse categories of salinity tolerance, as discussed above. I think it can be argued, with the emergence of panbiogeography and vicariance biogeography, that followers of those doctrines have tended to reject the freshwater fish salinity tolerance categories as of little relevance, since they tend also to generally reject, a priori, a role for dispersal in the establishment of the biotas of remote lands, whether or not the fish species can spend time at sea. Some of them have regarded the potential for survival in the sea as of no significance and have even attributed the very broad range of the large, brown marine macroalga, *Macrocystis*, complete with its buoyant, floating fronds, that is present in California and around the entire cold temperate Southern Ocean as a relict of old former land connections (Chin et al. 1991), but see Coyer et al. 2001); the notion has to be regarded as bizarre.

Rosen (1974: 322), for instance, was highly critical of biogeographers who "divide freshwater fishes into primary (restricted to freshwater) and secondary (salt tolerant) divisions, as suggested by Myers (1938) [Rosen commenting that] Hence the primary division ostariophysans and a few other fishes are to be 'trusted' in zoogeographic analysis, but the secondary ones are not." Rosen seemed unaware of, or perhaps he was disinterested in, the further categories discussed by Myers and others, and so did not bring into his discussion the role of regular migrations to and from the sea, as is true of diadromous fishes (but then he seemed unwilling to accept that galaxiids spend time at sea, anyway – see Chapter 8: *Galaxias* and Gondwana). His mind seemed closed to any perspective other than that pattern is a product of earth history. He seems to have regarded life at sea as irrelevant, and viewed the matter rather more simply, only recognising "continental and oceanic groups of fishes...the assignment to which is determined not by what we imagine to be the habits of the fishes and their possible dispersal mechanisms but by their distribution in relation to phylogeny and in relation to the distributions of other organisms." What this meant in practice is uncertain, and how this might help, Rosen failed to explain, and it is a mystery to me: why an understanding of a group's phylogenetic relationships should be the sole and final arbiter of how the distribution patterns of the taxa evolved is highly elusive. However, the pinnacle of the pursuit of these

arcane attitudes seems well passed for most biogeographers, and there is a rapidly growing, if not universal, acceptance of the role of dispersal in historical biogeography (de Queiroz 2005; Winkworth et al. 2005). Of particular present importance, the ability of freshwater fishes of some types to survive transoceanic dispersal has regained much of the biogeographical significance it had more than a century ago (Darwin 1873; Beddard 1895; Boulenger 1902; Regan 1905).

Though panbiogeographers have argued that there is no association between the geographical distributions of taxa and their ecologies (Croizat 1964; Grehan 1989), this is clearly contradicted by even the most simplistic examination of relationships between such metrics as geographical range and ability to fly (birds, insects), propagule size (orchid and other plant seeds, moss and fern spores), means of physical attachment (such as hooked, barbed or sticky seeds), the ability to swim through the sea (marine animals of diverse taxa) or, in the case of freshwater fishes, having life stages that regularly live in the sea (diadromous fishes – McDowall 1988; 2002b; McGlone 2006), and which are, thereby, able to disperse across broad ocean gaps during their marine life stages.

I explore these issues here for the history and ecology of the very well-known freshwater fish fauna in New Zealand (McDowall 1990, 2000), a fauna that is heavily dominated by the Galaxiidae, a family that is much the largest single element of the freshwater fish faunas both in New Zealand and other southern cool-temperate lands. The biogeography of this family has long attracted interest, and been controversial (Darwin 1873; Boulenger 1902; Darlington 1957, 1965; McDowall 1964, 1978, 1990, 2002b; Rosen 1974; Croizat et al. 1974; Campos 1984) (see Chapter 8).

5.6 The Place of Diadromy in the New Zealand Freshwater Fish Fauna

As is now clear, one of the fundamental issues explored in this book relates to the implications for biogeography of varying life history strategies that many of New Zealand's freshwater fishes normally undertake. And, while there may be something of a conceptual and methodological dichotomy between broad scale/historical patterns and local scale/ecological patterns, the present account reveals instances where ecology can influence distribution patterns over much broader spatial scales than does history. In particular, I show here that, in practice, some freshwater fishes can have essentially different geographical distribution patterns from other freshwater fishes, and that these differences are structured explicitly around life history strategies, related dispersal abilities, and thus ecology, i.e. historical biogeography is to a considerable extent mediated by ecology. To return to Myers (1949b) "The diadromous fishes, since they spend a part of their lives at sea, can be distributed by sea, which greatly reduces their usefulness in most terrestrial zoogeographic work." The biogeography of New Zealand's freshwater fish fauna, with its deep life history dichotomy between diadromous and non-diadromous species, provides an

important opportunity to achieve some partition of the roles of ecology and history, and it is one the purposes of the present account to do so.

These alternative life history strategies are not explicitly associated with different fish families: some species in all families in the New Zealand fauna are diadromous and regularly spend time at sea, whereas others may not. Various species included in the families Galaxiidae and Eleotridae belong to both life history types. Nor are the alternative strategies explicitly associated with monophyletic sub-groups within each family. In fact, there is a wide recognition that one of the processes that has contributed to speciation and diversification in the fauna has involved the abandonment of diadromy, and so there are several instances in which diadromous and non-diadromous species share common ancestries (McDowall 1969, 1970; Ling et al. 2001; Waters and Wallis 2001; Stevens and Hicks 2009). So, clearly, there is a distinct life history dichotomy between some closely related species, and in these species the distribution patterns relate more explicitly to ecology than they do to earth history.

Thus, I explore here these issues for the history and ecology of the very well-known freshwater fish fauna of New Zealand (McDowall 1990, 2000), a fauna that is heavily dominated by the Galaxiidae, a family that is much the largest single element in the freshwater fish faunas both in New Zealand and in other southern cool-temperate lands, and a family whose biogeography has long attracted interest, and been controversial (Darwin 1873; Boulenger 1902; Darlington 1957, 1965; McDowall 1964, 1978, 2002b; Rosen 1974; Croizat et al. 1974; Campos 1984).

5.7 The Nature of Diadromy

Diadromy is a term that was introduced to the lexicon of fish biology by Myers (1949a), who recognised the importance of life in the sea for diverse freshwater fishes, including particularly the role that diadromy might have had for biogeography. I have explored the implications of the various forms of diadromy for fish communities and biogeography in some depth (McDowall 1988, 1993; 1996a, 1997a, 1998a, b, 2003a, 2007a, b, 2008a, b, c, 2009a, b), and these implications emerge strongly in this book.

Diadromous fishes, as well as some gastropod molluscs and decapod crustaceans (McDowall 2007a, b, 2008b, and also including a New Zealand shrimp, *Paratya curvirostris*, f. Atyidae – Carpenter 1982) undertake seasonal migrations between the marine and fresh water biomes. A key element of these inter-biome migrations is their temporal, directional, life-stage and species-specific, regularity – which means that diadromous fishes are different from what are probably best referred to as facultative marine wanderers, i.e., species that tend to move between oceanic and fresh waters without much regularity or pattern, or which may sometimes move over brief time scales in synchrony with diurnal patterns of tidal flux, e.g., these species often enter river estuaries and lowland reaches from the sea on the rising tide and return to sea as the tide falls, and so spend relatively short periods in the lower reaches of freshwater rivers where salinities may be elevated by tidal

influence, anyway (McDowall 1988). These movements are structurally very different life histories and migrations from those of strictly diadromous species and have very different implications for osmoregulation owing to the brevity of the period spent in freshwater habitats.

As indicated above one of the key elements of diadromous migrations is their life stage/seasonal regularity. Furthermore, truly diadromous fish face a demanding, long-term, physiological challenge in making the freshwater/marine biome shift (in both directions) as they routinely live both in fresh water and at sea for months or more, and so must be able to adjust their physiologies to different osmoregulatory environments for quite prolonged periods (at least for months, if not longer). In some diadromous species the ability to successfully undertake prolonged osmoregulation in both marine and freshwater habitats is more generally present, regardless of fish size/growth stage and season of the year, and such fish can be described as euryhaline. They can enter and leave fresh waters at will. However in other, perhaps many, diadromous fishes the shift from one biome to the other is constrained by some quite explicit ontogenetic changes in their ability to osmoregulate and, as a result, the movements between biomes may be temporally- and life-stage-limited by transient physiological capability. Moreover, the biome shift may even be physiologically mandatory for the survival of individuals in some species, and they may have to do it at an explicit life stage/season of the year. Such fishes, Fontaine (1975) has described as amphihaline, and this rarely-made distinction from euryhaline is important.

Thus, an important distinction, between strictly diadromous species and facultative marine wanderers, is that the biome shift for individual fish in diadromous species is a long-term change, and so requires that the fish is able to make enduring, rather than temporary, adjustments to osmoregulatory performance. When living in fresh water they are tending to take in large volumes of fresh water to lower the electrolyte levels in their bodies, and to equilibrate with the habitat, and this takes both explicit ability and energy. Equally, when in the sea, they tend to dehydrate, losing water from their body tissues, again to reach an equilibrium with the habitat, and thus controlling this tendency, too, takes an explicit ability and energy, and regardless this is a costly matter for the fish. This is less true of euryhaline marine wanderers, because the inter-biome transition may be brief, so that longer-term osmoregulatory change is not necessary – moreover, such fish can usually leave fresh water and return to the sea (or vice versa) if they become physiologically stressed, or if they cannot, mortalities may follow – as was once recorded in the tidal but largely freshwater Lake Waihora, in southern New Zealand, where there was mortality of the kahawai, *Arripis trutta* (f. *Arripidae* – McDowall 1990), a primarily marine species that sometimes moves into the estuaries of large rivers, but cannot live there for long, and is certainly not diadromous.

Little is known about where most diadromous fishes fit among these categories of behaviour, whether various New Zealand species are euryhaline or amphihaline, but if our knowledge was more comprehensive I suspect that we would find a broad temporal continuum across the diversity of fishes, though I would expect significant abundance modes of both truly euryhaline and amphihaline fishes.

5.8 Different Sorts of Diadromy

Myers (1949a) defined three subcategories of diadromy, which vary in the directions and life stages of the various inter-biome migrations. From a biogeographical perspective, just knowing that diadromy takes place is probably the key element; occasionally, however, it is important to know which of the diadromous subcategories is implicated, and so they are briefly defined, below, and see Fig. 5.4.

5.8.1 Anadromous Fishes

Anadromous fishes are those that spend most of their lives in the sea, growing to maturity there, but which migrate into fresh water to breed; the main growth biome (the sea), is *different from* the reproductive biome (fresh water), and the biome shift from the sea to fresh water can be seen as a *breeding migration*.

Almost universally, species that are anadromous come into fresh water as mature adults, sometimes, though not necessarily, with fully developed gonads. Typically, anadromous migrants do not consume any food after they leave the sea, so that where maturation of the gonads takes place after migration, as it often does, maturation is driven entirely by the transfer of energy and nutrients from somatic tissues already available to the fish at migration, into the gonads. A concomitant implication is that body condition deteriorates as the gonads mature. In the pouched lamprey, it may take more than a year for full development of the gonads (McDowall

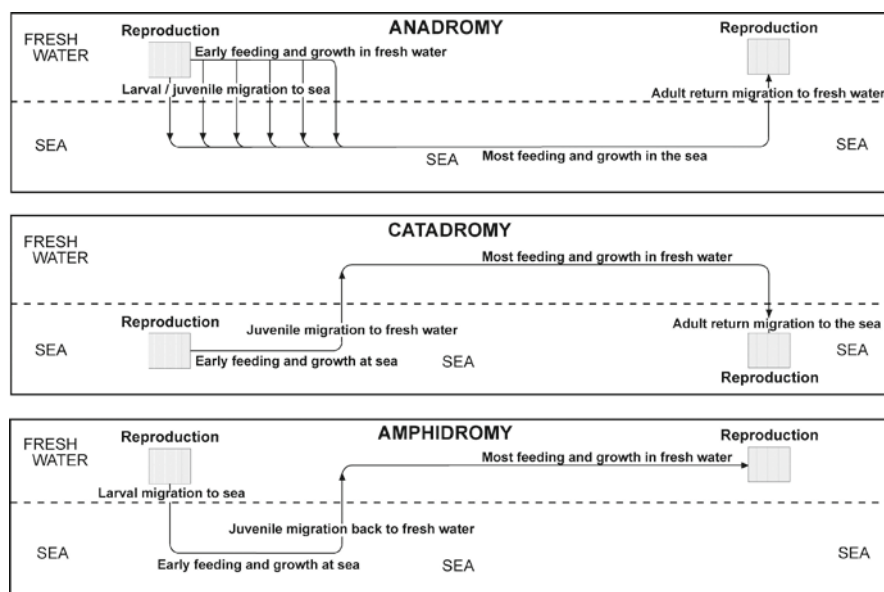


Fig. 5.4 Different forms of diadromy

2000), all of this at the expense of energy assimilated in the sea before migration. Anadromy is best known in the Northern Hemisphere salmon, smelts, sturgeons and shads, and is represented in New Zealand by the lamprey (Geotriidae) and two smelt species (Retropinnidae).

5.8.2 *Catadromous Fishes*

Catadromous fishes are those that spend most of their lives in fresh water, feeding and growing to maturity there, but which migrate to sea to breed; the main growth biome (fresh water) is again *different from* the reproductive biome (the sea), and the biome shift from fresh water to the sea can be seen as a *breeding migration*.

Issues relating to feeding and gonad development are similar to those in anadromous fishes, apart from the reversal of the biomes where these happen. Catadromous fish thus migrate to sea as fully grown adults, although the gonads are usually little developed. Some, at least, are believed not to feed at sea, at all, so that gonad development, again, takes place at the expense of energy and nutrients that the fish have sequestered in fresh water, prior to migration to sea. Catadromy is best known in the freshwater anguillid eels, that are present widely in the tropics and subtropics, and including the three anguillids in New Zealand.

5.8.3 *Amphidromous Fishes*

Amphidromous fishes are those that reproduce in fresh water and their larvae move to sea immediately on hatching; they spend their early (larval) lives at sea, but return to fresh water as small juveniles; they undertake further feeding, growth to maturity and they breed in fresh water; the main growth biome is *the same as* the reproductive biome (fresh water), and the biome shift from the sea back into fresh water is a *trophic migration* rather than a breeding one (definitions adapted from McDowall 1997a, 2004, 2007a). Amphidromy is best known, internationally, in the tropical and subtropical, mostly oceanic-island sicydiine gobies; in New Zealand there are amphidromous galaxiids, eleotrids, and others.

There is substantial confusion amongst ichthyologists particularly about amphidromy (Fig. 5.5), many mistakenly regarding it as a 'deviant' form of anadromy (e.g. Nelson 1994; Pauly 2004; Bell 2009), but it is really a very different life history strategy (McDowall 1997a, 2007a, b, 2009a, b). The particular point of difference in amphidromous fishes relates to their return migration to fresh water. As is true in anadromous fishes, spawning by amphidromous fishes takes place in fresh water, and also as in many (but far from all) anadromous fishes, the migration to sea is as newly hatched larvae. However, life at sea in amphidromous fishes is relatively brief, from a few weeks to a few months, and the return migration to fresh water is always as small juveniles, often <20 mm long and always, I think, less than about 55 mm. So life at sea is a relatively brief affair in amphidromous fishes, and

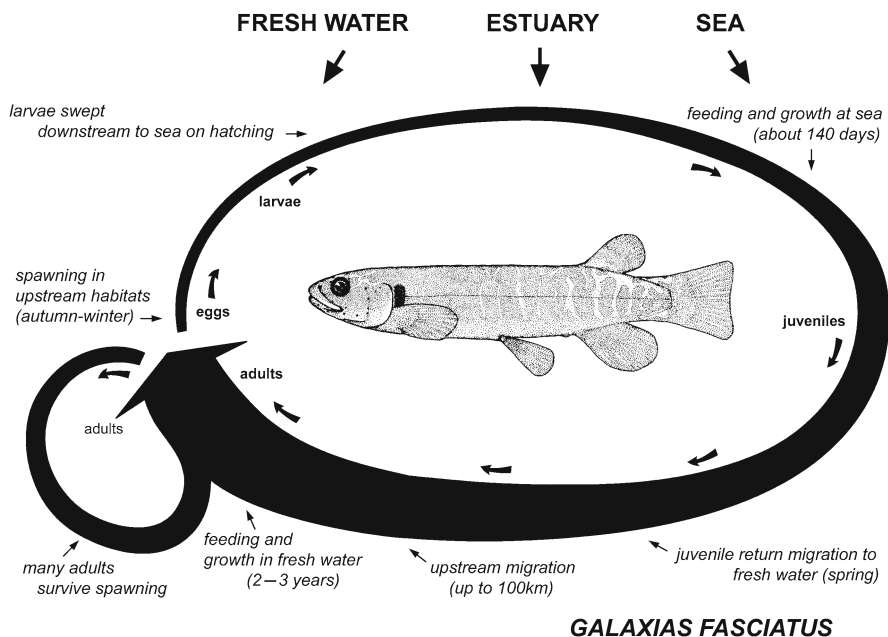


Fig. 5.5 The life history of an amphidromous species, *Galaxias fasciatus* (family Galaxiidae) from New Zealand

most of their feeding and growth take place in fresh water, after the return migration and these may take months, or even years. I believe this to be a finely-tuned life history strategy that has great advantages for species that inhabit the small, often highly isolated islands of the tropics and sub-tropics (McDowall 2009a, b), and its widespread presence in New Zealand is somewhat atypical for amphidromous fishes, generally. In some respects, amphidromy is more similar to catadromy than it is to anadromy, inasmuch as in both amphidromy and catadromy there is a migration of small juveniles into fresh water to feed, grow and mature, and that in both strategies most of the fishes' lives are spent in fresh water, whereas these life stages are largely marine in anadromous species.

Understanding these patterns of migration, their seasonality, and the size and migratory/climbing aptitudes of the fishes involved, may be of considerable importance to understanding their distribution patterns.

5.9 Diadromy in New Zealand Freshwater Fishes

In total, 18 New Zealand freshwater fish species are diadromous, and so this applies to about half the fauna – Table 1.1. The dichotomy between diadromy and non-diadromy needs to be recognised with some care as the implications for the

biogeography and ecology of the fauna are critically important. Interestingly, with the exception of the arrival of the Australian, spotted longfin eel in New Zealand fresh waters over the past 20 or more years (Jellyman et al. 1996; McDowall et al. 1998), and the two small ‘new’, probably adventive gobioid species, *Parioglossus marginalis* (see Fig. 1.9) and *Gobiopterus semivestitus* (McDowall 2001; McDowall and David 2008), recently recorded from New Zealand for the first time, all of the new taxa being recognised and/or described from New Zealand fresh waters over the past decade have been non-diadromous and non-migratory.

For species that are diadromous, the sub-category of their diadromy is indicated in Table 1.1. Among the 18 diadromous species in the fauna, one of them, the grayling, is long extinct (McDowall 1990) and is not considered here further in any detail, owing to our limited knowledge of its distribution – though what is known of its former range suggests that it would have exhibited the same types of distribution patterns and trends discussed below, as the other diadromous species do.

The implications of diadromy for distribution include:

1. Differences in the breadth of species’ ranges
2. Differences in downstream/upstream range and penetration of river systems
3. Substantial differences in which life stages are to be found in rivers and lakes

And, there are other patterns that emerge in the bulk of this book. Additional factors include the implications for (1) response to habitat perturbation across a broad range of temporal and spatial scales, and, (2) for local extirpation and the ability of species to recolonise area/habitats where there has been serious perturbation. Taken as a whole, I think that the presence/absence of diadromy is probably the main, broad-scale ecological/behavioural factor/attribute of the biogeography of the fauna as a whole.

5.10 Landlocking

Diadromy in some species seems highly facultative, and they are able to abandon their inter-biome migrations. The frequency with which populations of the various New Zealand species have abandoned diadromy, to become entirely freshwater-adapted, is of considerable interest to both ecology and distribution (there is nothing to suggest that any population of diadromous or freshwater species in the New Zealand fauna has made the opposite shift, becoming entirely marine, nor that any primarily freshwater-limited species has become diadromous), although it seems likely that some individual eels may spend much or all their lives in coastal seas, and never actually enter fresh water like most of their conspecifics.

Six normally diadromous New Zealand species are known to establish lacustrine populations:

1. Common smelt, koaro, and common bully do so often.
2. Banded kokopu and giant kokopu do so occasionally.

3. *Inanga* does so rarely in New Zealand (although it does so often in southeastern Australia, Patagonia and the Falkland Islands) (McDowall 1972, 1979, 1988, 1990; Northcote et al. 1992; Northcote and Ward 1985; McDowall et al. 2001; David et al. 2004).

Why there is this variation landlocking ability among the various species is unknown, and why landlocking is so common in *inanga* in Australia, Patagonia and the Falklands, but not in New Zealand, is unclear. For *inanga*, it could simply be that most New Zealand lakes, and especially those at low elevations and easily accessible to *inanga*, are very young (Lowe and Green 1987, 1992), and so there may have been less time for landlocked stocks to become established.

The adoption of an exclusively freshwater life has been undertaken by diadromous species in two ways:

- Sometimes the populations are in landlocked lakes, so that the diadromous migrations to and from the sea are physically prevented – often these are in lakes that were formed by landslides, natural or man-built dams, though sometimes lake formation may result from closure of lake outlets by coastal drift of gravel, and the fish populations in them were captured at lake formation.
- In other lakes, however, water continues to flow freely to sea, so that although diadromous migrations to and from the sea are physically possible, for some reason they do not happen; emigration may even vary among individuals, or from year to year, perhaps depending on the flushing rates of water from lakes. Failure to migrate to sea may be due partly to the larval fish being unable to find their way out of the lakes and so to sea, especially if outflow is from a large lake via a small outlet stream, and the rate of turnover of the water in the lake is slow, as may be true, for example, of Lakes Wairarapa, Waiholea or Ellesmere, all of which are quite large, shallow, low-elevation, coastal lakes through which there is relatively little flow.
- In some instances it is clear that lakes may actually have sympatric diadromous and non-diadromous populations of the same species (McDowall 1976; Northcote and Ward 1985; Hicks 1993; Closs et al. 2003; David, et al. 2004). Nor is there any reason to think that the diadromous and landlocked ‘stocks’ of such species sharing lakes are reproductively isolated from each other, and they may well reproduce together. In yet other lakes and wetlands considerable uncertainty remains about the migratory status of some of the fish populations. Or, the lake populations of the species may be variously diadromous when lake outlets permit migrations and associated biome shifts, and non-diadromous when the lake outlet is closed. Lake populations of diadromous species may sometimes be found at substantially higher elevations and distances inland than their migratory conspecifics (see red lines in Fig. 5.6), so the situation is quite variable and complex.

5.11 Implications of Loss of Diadromy for Speciation

It has long been recognised that one of the ways speciation has taken place in the New Zealand and other galaxiids has been through the abandonment of diadromy (McDowall 1970; Ovenden et al. 1993; Waters and Wallis 2001). Restriction of

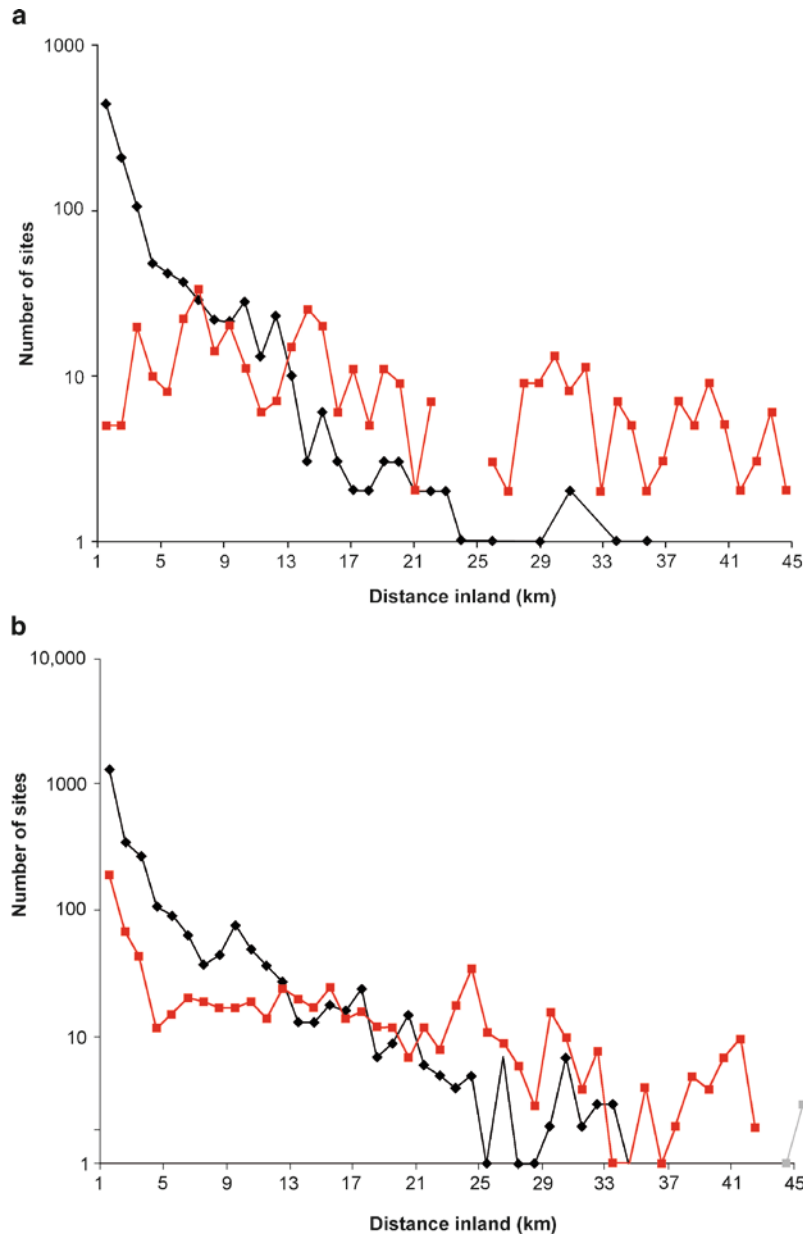


Fig. 5.6 Penetration profiles of diadromous (■) and non-diadromous (■) populations of: a. Koaro, *Galaxias brevipinnis*; and b. Common bully, *Gobiomorphus cotidianus*: the plots show lacustrine (non-diadromous) populations present much further inland than diadromous conspecifics

life to fresh water may have facilitated the interruption of gene flow in a manner helpful to subsequent divergence and the development of reproductive isolation. The various lineages in the *Gl. vulgaris* species complex are thought to be non-diadromous derivatives of the koaro (McDowall 1970; Waters and Wallis 2001) (see Chapter 11). Probably the same applies to the New Zealand *Neochanna* mudfishes, which form a sister group of the diadromous (amphidromous) Australian mudfish, *N. cleaveri* (Waters and McDowall 2005) (Chapter 14). Similar loss of diadromy is also evident in New Zealand's *Gobiomorphus* species, in which, again, various diadromous species are regarded as ancestral to various non-diadromous derivative species (McDowall 1975, 1990; Stevens and Hicks 2009) (Chapter 15).

There is, perhaps, a sense in which this process of biogeographical dispersal by a diadromous species into a new region, followed by the loss of diadromy and establishment of distinct non-diadromous species in freshwater ecosystems, is an analogue of the dispersal of flighted species, either birds or insects, followed by the divergence of derived species that are flightless or have limited powers of flight, a process that is widely known in island biotas (Darlington 1943; McLellan 1979; Trewick 1997, 2000; Trewick and Worthy 2000; Holdaway and Worthy 2006). Wallis and Trewick (2009) write of cosmopolitan forms with high gene flow [that] seem to have spawned propagules that have speciated into flightless local endemic, a process that has some parallels with the loss of diadromy. Are these dispersive diadromous fishes, then, among the "range extenders" that Gibbs (2006) discussed for New Zealand biogeography? There is a distinct irony in the loss or reduction of flight ability in island faunas, in the sense that in many instances island species have dispersed there, across ocean gaps, in substantial part mediated by their ability to fly (Gillespie et al. 2008), though the irony is shallow and an explanation relatively simple: loss of flight is occasioned in part by a loss of the need to fly to escape predators, and in part because many islands are in windy localities and flying makes small animals especially vulnerable to being swept out to sea, with fatal results. Much the same might be said of the loss of diadromy in which there seem likely to be problems of juvenile recruitment into fresh water from the ocean, and the abandonment of diadromy resolves that problem.

Restoration of diadromy, once entirely lost, seems likely to be difficult/rare – there are no known instances in New Zealand's freshwater fishes, though it appears sometimes to be true of some northern, high latitude salmonids (McDowall 1988; Waters and Wallis 2001); however, little is known.

5.12 Implications of Diadromy for Life History/Demography

Although the question has not yet been addressed in detail, there are some interesting patterns that relate to fish population demographic elements such as egg and larval size, fecundity, and spawning season (McDowall 1970, 1990). In general, diadromous species tend to grow much larger than their non-diadromous congeners, at least in both New Zealand Galaxiidae and Eleotridae. Among the diadromous galaxiids, spawning tends to be in autumn and early winter, fecundity is high,

and egg size tends to be relatively small, with the larvae being correspondingly of small size. This means that the very numerous small larvae are emigrating to sea and spend all, or much, of the winter there. They have access to the trophically rich marine plankton, where there are abundant planktonic foods of small size, though these diadromous fish species seem highly vulnerable to expatrial dispersal in ocean currents (McDowall 2009b), and mortalities may be high in the marine plankton. There is likely to be higher availability of small food organisms in the marine plankton than in freshwater streams, though perhaps there are higher mortalities at sea from predation and expatrial dispersal. At least the well-grown juveniles of New Zealand's diadromous *Galaxias* species mostly return to fresh waters during the spring. However, the tropical and sub-tropical sicydiine gobies, which are widely amphidromous, seem to spawn year-round (Iida et al. 2009). So, in diadromous species there is an 'r-selected' strategic response (Pianka 1970; Reznick et al. 2002) to high rates of dispersion resulting from migrations to and from the sea and early life there (McDowall 1970; McIntosh and McDowall 2004).

In contrast, non-diadromous galaxiids tend to reach smaller absolute size as adults, they spawn in the later winter and spring, they tend to have relatively larger eggs and lower fecundity than in diadromous species, and so a more 'K-selected' life history strategy. The relatively larger eggs result in larger larvae, providing advantages in relation to early larval food availability in freshwater ecosystems, partly, also, providing stronger swimming ability to help them to maintain position in fluvial habitats and the latter attribute is of particular relevance to New Zealand's steep topography and, often swift-flowing, gravelly streams. Interestingly, Wowor et al. (2009) point to an ancestral state in amphidromous *Macrobrachium* shrimps (f. Palaemonidae) that have small numerous eggs, but fewer, larger eggs in species that have abandoned amphidromy.

This temporal spawning dichotomy, and particularly the spring spawning of non-diadromous species, may be driven by the need for new cohorts to reach a minimal size that allows them to overwinter in fresh water in their first year (Shuter and Post 1990), this perhaps being of particular importance for many non-diadromous species, which tend to be found at higher elevations where temperatures are colder, especially in winter. Diadromous species may escape this restriction by spending their first winter at sea (McDowall 1970). Interestingly, cold-temperate, Northern Hemisphere salmonids, though they often spawn in autumn and winter, tend also to time their spawning so as to have their young emerging into stream ecosystems during spring as water temperatures are beginning to rise, again maximising the growth period available to them prior to facing the looming cold winter (Elliott 1994; Behnke 2002). The large eggs of these fish are endowed with high yolk volumes to allow long, slow development over the cold winters. A diadromous life history, at least in the autumn/winter spawning diadromous galaxiids, also means that the progeny are large- and vigorous-enough swimmers at return to fresh water to manage the flowing waters of rivers and streams and are large enough to find prolific animal foods in the benthic riverine faunas.

The demographics of the diadromous/nondiadromous species of bullies (*Gobiomorphus* spp.) are perhaps even more divergent, though the same principles apply. All diadromous (amphidromous) *Gobiomorphus* species are spring spawners,

whereas non-diadromous species spawn across the spring and summer. The diadromous species have numerous small eggs and their larvae go to sea; nondiadromous fluvial species have much larger but many fewer eggs and so larger, more vigorous-swimming fry (McDowall 1990). Though equally fascinating from the perspective of life history evolution, further pursuit of questions of egg size/egg number and spawning season, is beyond the present analysis, but these questions provide an interesting and fertile challenge for future work.

In both galaxiids and eleotrids, there are also, non-diadromous but lacustrine populations of otherwise diadromous species. Life history strategies in lacustrine species, and lacustrine populations of otherwise diadromous species, tend to have life history attributes similar to diadromous populations/species, with numerous small eggs, and tiny larvae that are pelagic in the surface waters of lakes, where they are plankton predators, and so live in the surface waters of lakes in much the same way as their diadromous conspecifics are planktonic at sea.

5.13 Implications for Biogeography

It has long been apparent to me that dual and distinctive patterns in the distributions exhibited by New Zealand's freshwater fishes relate variously to both their ecologies and/or their histories (McDowall 1964, 1978, 1990, 1996a, b, 1997b, 1998a, b, 2002b; McDowall and Whitaker 1975). One of the primary goals of the present book is to demonstrate that, as suggested by Wiens and O'Donoghue (2004), it is, at least sometimes, possible to unravel the distinctive roles of ecology (especially life history strategies) and earth history (geology and geomorphology) as determinants of observed distribution patterns in a biota. Unlike Craw (1979, 1989), Page (1989), Grehan (1989), Michaux (1998), Heads and Patrick (2003), and others, I show that pattern *is* related to process, and that there are deep divergences in distribution patterns between fish species with different ecological/life history strategies. In particular, I show that key aspects of the origins, derivations, and especially distribution patterns of that fauna relate explicitly to whether various groups of species do, or do not, exhibit diadromous (sea-migratory) life history strategies (McDowall 1988, 1996a, b, 1998a, b, 2008b), i.e. to their ecology.

Viewed broadly, diadromy and life history strategies, generally, may be seen to have wide ranging and fundamental implications for the biogeographies and ecologies of New Zealand's freshwater fishes. Specifically, the predictions, listed below, specify some explicit patterns of occurrence that distinctively reflect the roles of history and ecology (dispersal) in the biogeographies of the taxa. This dichotomy probably exists in all freshwater fish faunas, but partitioning them in the way I have been able to in the present study for New Zealand, may be demanding or impossible owing to a lack of knowledge. However, the same principles seem likely to apply. To me, this all appears like "common sense" (Ebach and Humphries 2003), though for some reason the panbiogeographers, cladistic and vicariance biogeographers seem to demur. I think they are simply wrong.

- For species that are diadromous an explanation of their broad-scale distributions lies explicitly in their behaviour, and relates substantially to historical and contemporary dispersal through the sea (ecology); this also has significant implications for the community assembly and structure, and the ecology of the fauna.
- For those that are not diadromous, explanations of their local-scale distributions may lie largely in vicariance, and specifically in the species' historical responses to geology (earth history).

I aim here to take these questions a step further than hitherto. This dichotomy in what drives pattern has, at its roots, an understanding of the life histories (ecology) of the species in the fauna. Moreover, it is important to understand that this life history dichotomy does not always partition the fauna into phylogenetically related groups, but sometimes divides the fauna across species groups in which, as noted above, diadromous and non-diadromous species share common ancestries. Thus, species in monophyletic groups in the fauna may have quite divergent life histories, and equally disparate, biogeographical/distributional histories. Basically, I demonstrate, in practice, what is clearly evident in principle, that both history and ecology are major drivers of distribution patterns, and that the biogeography of the New Zealand freshwater fish fauna can be partitioned substantially by alternative life history strategies (i.e. ecology). In that sense, demands by Rosen's (1974) and other vicariance and cladistic biogeographers for biogeography to be linked explicitly to phylogeny breaks down in disarray.

5.14 Some Predictions

The recognition that there are these variously independent, dual, influences of ecology and history upon biotic distributions in the New Zealand freshwater fish fauna, and in particular the role of diadromy (and I suspect this is true globally), prompts a number of predictions (McDowall 1993, 1996a, b, 1998a, b; McDowall and Taylor 2000):

- (i) Diadromous species will have biogeographical commonalities driven by life histories; they are capable of spending time in the sea, and regularly do so in each individual fish's life span (McDowall 1988, 1990); they will tend to be much more widespread across the latitudes of New Zealand than non-diadromous species that cannot/do not live at sea.
- (ii) Despite being latitudinally more widespread, diadromous species will exhibit downstream-upstream distribution patterns within individual river systems that reflect several features:
 - (a) Their distributions will tend to be positively skewed across altitudes and the species will tend to be much more widespread and abundant at low elevations and short distances inland from the sea, though there will also be the influence of the distributions of the different, preferred habitat types.
 - (b) Diadromous species' distributions will differ, relating to interspecific differences in their migratory capacities and their instincts to migrate

upstream, so that the downstream/upstream patterns of occurrence in river systems will differ among species.

- (c) As well, these diadromous species will tend to be absent upstream of both natural and anthropogenic barriers to migrations, like torrents, falls and dams (or will be less abundant there, as some species can climb falls and dams; McDowall 1990, 2003b).
- (d) Events like periodic river-mouth or lake-outlet closure may prevent recruitment of diadromous species into freshwater habitats, leading to temporally distorted age structures of populations and, if closure is long-lasting, eventually local extirpation (except where landlocked populations become established).
- (e) Diadromous species will tend to exhibit low within-taxon/among-population genetic structuring owing to easy the gene flow that results from movements between river systems through coastal seas.
- (f) Congeneric diadromous species will tend to be widely, mutually sympatric, as well as sometimes being sympatric with some non-migratory ones.
- (g) Diadromous species will also tend to have distributions that do not reflect historical, geological/geomorphological changes and perturbations in the New Zealand landscape owing to their ability to re-invade river systems from the sea once these changes and/or perturbations have dissipated.
- (h) Lake-limited ('landlocked') populations are known for several diadromous species (six of the 17 extant diadromous species in the New Zealand freshwater fish fauna), and the patterns of distribution and abundance of such lake populations across elevations and distances inland, may differ from those of their diadromous conspecifics.
- (i) Distributions of landlocked stocks will relate substantially to the accessibility of lakes to the fish, migrating upstream from the sea, that would originally have founded such populations and, further:
- (j) Hence, depending on (i) above, the elevation profiles of habitats occupied by lake populations may exceed (or otherwise differ from) those of their diadromous conspecifics (as mentioned earlier, and Fig. 5.6; also see Fig. 18.3).

Different patterns will emerge for non-diadromous species:

- (i) They may have narrower latitudinal ranges, and they may be present further inland and at higher elevations than diadromous species.
- (ii) There will not necessarily be downstream-upstream distribution patterns of increasing frequency of occurrence and/or abundance.
- (iii) They may, or may not, have distributions that are linked to proximity to the coastline, and their 'centres of occurrence/abundance' will tend to be highly varied as to latitude and distance inland; site elevations and distances inland where these species are found may tend to be more normally distributed rather than strongly positively skewed.
- (iv) They can occur in places where access from the sea, or downstream in rivers, is not currently possible, as above major falls, or in water bodies that are

disconnected from other aquatic systems (like small, isolated lakes or wetlands).

- (v) Each species will also tend to exhibit greater population genetic structuring across its geographical range, on account of lower levels of gene flow among populations that may have to depend on new fluvial connections or other dispersal mechanisms.
- (vi) These non-migratory species will often have narrower latitudinal ranges, but may exhibit less within-population genetic diversity, perhaps due to population bottlenecks.
- (vii) There will be less sympatry among non-migratory congeneric species, especially those that share common ancestries, given that most speciation is allopatric (Mayr 1963), and also given that ecologically similar species will tend to not co-occur for reasons relating to resource competition.
- (viii) Non-diadromous species may tend to share common ancestries with diadromous congenics, as some speciation processes are driven by diadromous species abandoning their migrations to and from the sea, leading to them spending their whole lives in fresh water, and becoming genetically and reproductively isolated from sister taxa as a result of geography: this will result in, or allow, genetic, morphological, and behavioural divergence (McDowall 1970, 1988, 1990; Waters and Wallis 2001; Gleeson et al. 1998, 1999; Ling et al. 2001).
- (ix) The distributions of non-diadromous species, and also the patterns of phylogenetic relationships among them, may tend to reflect past geological/geomorphological events in New Zealand's history as they lack the easy ability to reinvade once extirpated (at least when compared with reinvasion by diadromous species).

Thus, viewed broadly, these patterns are likely to have implications for community structuring and assembly.

- Diadromous species are likely to be more speciose at low elevations, and their patterns of community species richness are predicted to exhibit a decline at increasing elevations and distances inland from the coast.
- In contrast, non-diadromous species are unlikely to exhibit general patterns of changing species richness that correlate with elevation and distances inland from the sea.

Much of the rest of the book explores these predictions.

References

- Allen KR (1956) The geography of New Zealand's freshwater fish. *N Z Sci Rev* 14(3):3–9
- Bănarescu P (1995) Zoogeography of fresh waters, Vol. 3. Distribution and dispersal of freshwater animals in Africa, Pacific areas and South America. AULA-Verlag, Wiesbaden, Germany, pp 1103–1617

- Beddard FE (1895) A text-book of zoogeography. Cambridge University Press, Cambridge, 246 pp
- Behnke RJ (2002) Trout and salmon of North America. Chanticleer Press, New York, 359 pp
- Bell KNI (2009) What comes down must go up: the migration cycle of juvenile-return anadromous taxa. *Am Fish Soc Symp* 69:321–341
- Boulenger GA (1902) The explanation of a remarkable case of geographical distribution among fishes. *Nature* 67:84
- Boulenger GA (1905) The distribution of African freshwater fishes *Nature* 72:413–421
- Burgess GH (1989) Zoogeography of the Antillean freshwater fish fauna. In: Wood CA (ed) *Biogeography of the West Indies: past, present and future*. Sand Hill Crane Press, Gainesville, FL, pp 263–304
- Burridge CP, Craw D, Waters JM (2006) River capture, range expansion, and cladogenesis: the genetic signature of freshwater vicariance. *Evol* 60:1038–1049
- Campos H (1984) Gondwana and neotropical galaxioid fish biogeography. In: Zaret T (ed) *Evolutionary ecology of neotropical freshwater fishes*. Junk, The Hague, The Netherlands, pp 113–125
- Carpenter A (1982) Habitat and distribution of the freshwater shrimp *Paratya curvirostris* (Decapoda: Atyidae). *Mauri Ora* 10:85–98
- Chin NKM, Brown MT, Heads MJ (1991) The biogeography of *Macrocystis*. *Hydrobiologia* 215:1–11
- Closs GP, Smith M, Barry B, Markwitz A (2003) Non-diadromous recruitment in coastal populations of common bully (*Gobiomorphus cotidianus*). *N Z J Mar Freshwater Res* 37:301–310
- Coyer JA, Smith GG, Anderson RA (2001) Evolution of *Macrocystis* (Phaeophyceae) as determined by ITS1 And ITS2 sequences. *J Phycol* 37:574–585
- Craw RC (1979) Generalized tracks and dispersal in biogeography: a response to RM McDowall. *Syst Zool* 28:99–107
- Craw RC (1989) New Zealand biogeography: a panbiogeographic approach. *N Z J Zool* 16:527–547
- Craw D, Burridge CP, Upton P, Rowe DL, Waters JM (2008) Evolution of dispersal corridors through a tectonically active mountain range in New Zealand. *J Biogeogr* 35:1790–1802
- Croizat L (1964) Space, time, form: the biological synthesis Publ Author. Caracas, Venezuela, 881 pp
- Croizat L, Nelson GJ, Rosen DE (1974) Centers of origin and related concepts. *Syst Zool* 23:265–287
- Darlington PJ (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas and on atrophy of wings. *Ecol Monog* 13:37–61
- Darlington PJ (1957) *Zoogeography: the geographical distribution of animals*. Wiley, New York, 675 pp
- Darlington PJ (1965) *Biogeography of the southern end of the world*. Harvard University Press, Cambridge, MA, 235 pp
- Darwin C (1873) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, 6th edn. Murray, London, 458 pp
- David B, Chadderton L, Closs G, Barry B, Markwitz A (2004) Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*). *DOC Science Int Ser* 160:1–23
- de Queiroz A (2005) Resurrection of oceanic dispersal in historical biogeography. *Trends Ecol Evol* 20:68–73
- Ebach M, Humphries CJ (2003) Ontology of biogeography. *J Biogeogr* 30:959–962
- Eldon GA (1992) The galaxiids of New Zealand. *Trop Fish Hobbyist* 40:98–111
- Elliott JM (1994) *Quantitative ecology and the brown trout*. Oxford University Press, London, 286 pp
- Filipe AF, Araujo MB, Doadrio I, Angermeier PL, Collares-Pereira MJ (2009) Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. *J Biogeogr* 36:2096–2110

- Fontaine M (1975) Physiological mechanisms in the migrations of marine and amphihaline fish. *Adv Mar Biol* 13:241–335
- Gibbs GW (2006) Ghosts of Gondwana: a history of life in New Zealand. Craig Potton, Nelson, N Z, 232 pp
- Gillespie RG, Claridge EM, Roderick GK (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Mol Ecol* 17:45–57
- Gleeson DM, Howitt RLJ, Ling N (1998) Phylogeography of the black mudfish, *Neochanna diversus* (Galaxiidae). *Geol Soc N Z Misc Pub* 97:27–30
- Gleeson DM, Howitt RLJ, Ling N (1999) Genetic variation, population structure and cryptic species within the black mudfish, *Neochanna diversus*, an endemic galaxiid from New Zealand. *Mol Ecol* 8:47–57
- Grehan JR (1989) New Zealand panbiogeography: past, present and future. *N Z J Zool* 16: 513–525
- Heads MJ, Patrick B (2003) Biogeography. In: Darby J, Fordyce RE, Mark AF, Probert K, Townsend C (eds) The natural history of southern New Zealand. Otago University Press, Dunedin, N Z, pp 89–100
- Helfman G, Collette BB, Facey D (1997) The diversity of fishes. Blackwell, Malden, MA, 512 pp
- Hicks BJ (1993) Investigation of the fish and fisheries of the Lake Wairarapa wetlands. *N Z Freshwater Fish Misc Rep* 126:1–77
- Holdaway RN, Worthy TH (2006) Evolution of New Zealand and its vertebrates. In: Merrick JR, Hickey AM, GM LMSY (eds) Evolution and biogeography of Australasian vertebrates. Auscipubs, Oatlands, NSW, pp 111–128
- Hynes HBN (1970) The ecology of running waters. Liverpool University Press, Liverpool, 555 pp
- Iida N, Watanabe S, Tsukamoto K (2009) Life history characteristics of a scydiine goby in Japan compared with its relatives and other amphidromous fishes. *Amer Fish Soc Symp* 69:355–373
- Jellyman DJ, Chisnall BL, Dijkstra LH, Boubée JAT (1996) First record of the Australian long-finned eel, *Anguilla reinhardtii*, in New Zealand. *Mar Freshwater Res* 47:1037–1040
- Kinzie RA (1988) Habitat utilization by Hawaiian stream fishes with reference to community structure in oceanic island streams. *Environ Biol Fish* 22:179–192
- Lapsley P (1993) Alas, poor zebra. *Salmon, Trout and Sea Trout* October 1993:64–67
- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species: the ‘new’ biodiversity and evolutionary significant units among New Zealand’s galaxiid fishes. *J Fish Biol* 59(Suppl A):209–222
- Loope LL, Mueller-Dombois D (1989) Characteristics of invaded islands, with special reference to Hawaii. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds) Biological invasions: a global perspective. Wiley, New York, pp 257–280
- Lowe DJ, Green JD (1987) Origin and development of the lakes. In: Viner A (ed) Inland waters of New Zealand. *N Z Dep Sci Indust Res Bull* 241:1–64
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 107–143
- Lucas MC, Baras E (2001) Migrations of freshwater fishes. Blackwell Science, Oxford
- Mayr E (1963) Animal species and evolution. Belknap, Cambridge, MA, 797 pp
- McDowall RM (1964) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1969) Relationships of the galaxioid fishes and a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool, Harv Univ* 139:341–431
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *J R Soc N Z* 2:325–367

- McDowall RM (1975) A revision of the New Zealand species of *Gobiomorphus* (Pisces: Eleotridae). *Natl Mus N Z Rec* 1:1–32
- McDowall RM (1976) Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J R Soc N Z* 6:17–22
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1979) Fishes of the family Retropinnidae (Pisces: Salmoniformes): a taxonomic revision and synopsis. *J R Soc N Z* 9:85–121
- McDowall RM (1988) Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London, 309 pp
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1993) Implications of diadromy for the structuring and modelling of riverine fish communities in New Zealand. *N Z J Mar Freshwater Res* 27:453–462
- McDowall RM (1995) Seasonal pulses in migrations of New Zealand diadromous fish and the potential impacts of river mouth closure. *N Z J Mar Freshwater Res* 29:517–526
- McDowall RM (1996a) Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Can J Fish Aquat Sci* 53(suppl 1):219–236
- McDowall RM (1996b) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1997a) Is there such a thing as amphidromy? *Micronesica* 30:3–14
- McDowall RM (1997b) The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Rev Fish Biol Fisher* 7:443–462
- McDowall RM (1998a) Driven by diadromy: its role in the historical and ecological biogeography of New Zealand freshwater fishes. *Ital J Zool* 65(Suppl S):73–85
- McDowall RM (1998b) Fighting the flow: downstream-upstream linkages in the ecology of diadromous fish faunas in West Coast New Zealand rivers. *Freshwater Biol* 40:111–122
- McDowall RM (2000) Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 216 pp
- McDowall RM (2001) *Parioglossus* (Teleostei: Microdesmidae) in New Zealand. *N Z J Mar Freshwater Res* 35:165–172
- McDowall RM (2002a) The origin of the salmonid fishes: marine, freshwater...or neither. *Rev Fish Biol Fisher* 11:171–179
- McDowall RM (2002b) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2003a) Hawaiian biogeography and the islands' freshwater fish fauna. *J Biogeogr* 30:703–710
- McDowall RM (2003b) The key to climbing in the koaro. *Wat Atmosf* 11(1):16–17
- McDowall RM (2004) Ancestry and amphidromy in island freshwater fish faunas. *Fish Fisher* 5:75–85
- McDowall RM (2007a) Hawaiian stream fishes: the role of amphidromy in history, ecology and conservation biology. In: Evenhuis NL, Fitzsimons JM (eds). *Biology of Hawaiian streams and estuaries*. Bishop Mus Bull Cult Environ Stud 3:3–9
- McDowall RM (2007b) On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish Fisher* 7:1–13
- McDowall RM (2008a) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM (2008b) Diadromy, history and ecology: a question of scale. *Hydrobiologia* 602:40–14
- McDowall RM (2008c) Why are so many boreal freshwater fishes anadromous: Confronting 'conventional wisdom'? *Fish Fisher* 9:1–6
- McDowall RM (2009a) Early hatch: a strategy for safe downstream larval transport in amphidromous fishes. *Rev Fish Biol Fisher* 19:1–8
- McDowall RM (2009b) Why be amphidromous: expatrial dispersal and the place of source and sink population dynamics. *Rev Fish Biol Fisher* 20:87–100

- McDowall RM, David BO (2008) *Gobiopertus* in New Zealand (Teleostei: Gobiidae) with observations on sexual dimorphism. *N Z J Mar Freshwater Res* 42:325–331
- McDowall RM, Taylor MJ (2000) Environmental indicators of habitat quality in a migratory freshwater fish fauna. *Environ Manag* 25:357–374
- McDowall RM, Whitaker AH (1975) The freshwater fishes. In: Kuschel G (ed) *Biogeography and ecology in New Zealand*. Junk, The Hague, The Netherlands, pp 277–299
- McDowall RM, Jellyman DJ, Dijkstra LC (1998) Arrival of an Australian anguillid eel in New Zealand: an example of transoceanic dispersal. *Environ Biol Fish* 51:1–6
- McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands freshwater fishes. *Aquatic Conserv Mar Freshwater Ecosyst* 11:473–486
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of the biota. *Ecolog Stud* 186:17–32
- McIntosh AR, McDowall RM (2004) Fish communities in rivers and streams. In: Harding JS, Mosley MP, Pearson CP, Sorrell BK (eds) *Freshwaters of New Zealand*. New Zealand Hydrological and Limnological Societies, Christchurch, N Z, pp 17.1–17.9
- McLellan ID (1979) New Zealand terrestrial stoneflies and some ideas on speciation. *Proc Plecoptera Sympos Gewas Abwas* 64:56–59
- Michaux B (1998) Terrestrial birds of the Indo-Pacific. In: Hall R, Holloway JD (eds) *Biogeography and geological evolution of SE Asia*. Backhuys, Leiden, The Netherlands, pp 361–392
- Myers GS (1938) Fresh-water fishes and West-Indian zoogeography. *Smithson Rep* 1937:339–364
- Myers GS (1949a) Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia* 1949:89–97
- Myers GS (1949b) Salt tolerance of fresh-water fish groups in relation to zoogeographical problems. *Bijdr Dierk* 28:315–322
- Myers GS (1951) Fresh-water fishes and East Indian zoogeography. *Stanf Ichthyol Bull* 4:11–21
- Nelson JS (1994) *Fishes of the world*. Wiley, New York, 600 pp
- Nelson JS (2006) *Fishes of the world*, 4th edn. Wiley, New York, 601 pp
- Nichols JT (1928) *Fishes of the White Nile*. *Amer Mus Novit* 319:1–7
- Northcote TG, Ward FJ (1985) Lake resident and migratory smelt *Retropinna retropinna* (Richardson), of the lower Waikato River system. *N Z J Mar Freshwater Res* 17:113–129
- Northcote TG, Hendy CH, Nelson CS, Boubée JAT (1992) Tests for migratory history of the New Zealand common smelt (*Retropinna retropinna* (Richardson)) using oxygen isotopic composition. *Ecol Freshwater Fish* 1:61–72
- Ovenden JR, White RWG, Adam M (1993) Mitochondrial and allozyme genetics of two Tasmanian galaxiids (*G. auratus* and *G. tanycephalus*: Pisces: Galaxiidae) with restricted lacustrine distributions. *Heredity* 70:223–230
- Page RDM (1989) New Zealand and the new biogeography. *N Z J Zool* 16:471–484
- Pauly D (2004) *Darwin's fishes: an encyclopaedia of ichthyology, ecology and evolution*. Cambridge University Press, Cambridge, 340 pp
- Pianka ER (1970) On r- and K-selection. *Am Nat* 104:592–597
- Pringle CM (1997) Exploring how disturbance is transmitted upstream. *J N Am Benth Soc* 16:425–438
- Radtke RL, Kinzie RA (1991) Hawaiian amphidromous gobies: perspectives on recruitment processes and life history events. In: Devick WL (ed) *New directions in research, management and conservation of Hawaiian stream fishes: proceedings of the 1990 symposium on freshwater stream biology and fisheries management*. Division of Aquatic Resources, Department of Land Management, Honolulu, HA, pp 125–141
- Regan CT (1905) A revision of the fishes of the family Galaxiidae. *Proc R Soc, Lond* 2:363–384
- Resh VH, Szalay FA (1995) Streams and rivers of Oceania. In: Cushing GE, Cummins CE, Minshall GW (eds) *Ecosystems of the world 22: River and stream ecosystems*. Elsevier, Amsterdam, The Netherlands, pp 717–739

- Reznick D, Bryant M, Bashey F (2002) r- and K-selection revisited: the role of population regulation in life history evolution. *Ecology* 83:1509–1520
- Rosen DE (1974) Phylogeny and zoogeography of salmoniform fishes and the relationships of *Lepidogalaxias salamandroides*. *Bull Am Mus Nat Hist* 153:265–326
- Sax D, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands, worldwide: a comparative study of plants and birds. *Am Nat* 160:766–783
- Serventy DL, Raymond R (1980) *Lakes and rivers of Australia*. Sunset Books, Sydney, NSW, 160 pp
- Shuter B, Post J (1990) Climate, population viability, and the zoogeography of temperate fishes. *Trans Am Fish Soc* 119:314–336
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Stokell G (1950) Freshwater fishes from the Auckland and Campbell Island. *Cape Exped Ser Bull, N Z Dep Sci Industr Res* 9:1–8
- Stokell G (1953) The distribution of the family Galaxiidae. *Proc 7th Pac Sci Congr* 4:48–52
- Trewick SA (1997) Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Phil Trans R Soc (Biol Sci)* 352:429–446
- Trewick SA (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *J Biogeogr* 27:1189–1200
- Trewick SA, Worthy TH (2000) Origins and prehistoric ecology of takahe, flightless *Porphyrio* (Aves: Rallidae). In: Lee WG, Jamieson IG (eds) *The takahe: 50 years of conservation management and research*. Otago University Press, Dunedin, N Z, pp 31–48
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CF (1980) The river continuum concept. *Can J Fish Aquat Sci* 37:130–137
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:415–425
- Waters JM, Wallis GP (2000) Across the Southern Alps by river capture? Freshwater fish phylogeography in South Island, New Zealand. *Mol Ecol* 9:1577–1582
- Waters JM, Wallis GP (2001) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid fish lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Wiens JJ, O'Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19:640–644
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Div Evol* 5:327–247
- Wowor D, Muthu V, Meier R, Balke M, Cai Y, Ng PKL (2009) Evolution of life history traits in Asian freshwater prawns of the genus *Macrobrachium* (Crustacea: Palaemonidae) based on multilocus molecular phylogenetic analysis. *Mol Phyl Evol* 52:340–350

Chapter 6

Data Sources for the Present Study

Abstract Data on the distributions of New Zealand freshwater fishes derive from the New Zealand freshwater fish database, an historical archive on the occurrence of these fishes throughout the country, with about 25,000 sites now included in the database, beginning in the 1960s. A gazetteer provides information on New Zealand place names and geography, to assist comprehension of the patterns of distribution.

Keywords Distribution • Freshwater fish database • Gazetteer • Geography • Placenames

6.1 Taxonomic Status of the Fauna

As with any biogeographical study, this book is substantially structured around the state of knowledge of the taxonomy of the subject fauna. In the present instance, the freshwater fish fauna dealt with here has been reviewed in detail in McDowall (1990, 2000), with several additional species described since these reviews (Mitchell 1995; Ling and Gleeson 2001; McDowall and Waters 2002, 2003; McDowall and Chadderton 1999). In addition, the species described by Mitchell (1995) as belonging in the genus *Galaxias*, has been re-assigned to the genus *Neochanna* (McDowall 2004). As well as these explicitly taxonomic treatments, there has been extensive molecular work that has revealed additional genetic lineages for which decisions on taxonomic status are still awaited (see McDowall and Hewitt 2004; McDowall 2006).

6.2 Data Sources on Distribution

The distributions of New Zealand's freshwater fish fauna are now relatively well understood. Information on the distributions of species in the fauna used in this study is derived primarily from the NIWA New Zealand Freshwater Fish Database

The database itself is accessible to registered users through the internet at:

<http://www.niwa.co.nz/services/free/nzffd>

Approval for access to the database can be obtained by application to the database manager at:

fwdba.niwa.co.nz

Access to the database is free of charge, although there is an expectation (not always fulfilled!) that those who use the database will also contribute to it. In addition to the database itself, there is a 'database assistant' programme, developed by Ian Jowett, formerly employed at the Hamilton campus of the National Institute of Water and Atmospheric Research. This programme is available for producing maps, and for derivation and processing of data from the database, providing information on species' distributions, communities present, and often information on habitat parameters. Maps presented in this book were in general produced using this computer programme.

The management of the database itself has no involvement in undertaking data acquisition, through faunal surveys or in site sampling, but is entirely an archive for the storage of any information on freshwater fish species collected for other purposes by any agencies willing to contribute that are actively undertaking freshwater research in New Zealand. These organisations are typically involved in research and management activities, mostly undertaken by diverse government departments, regional councils with responsibility for managing rivers and lakes, universities, crown research institutes, environmental consultancies and other agencies and some private individuals involved in New Zealand freshwater fish studies. This means that there is no structured or managed basis for the collection of data in such a way as to ensure that the database provides representativeness across temporal and geographical scales, or from taxonomic perspectives.

The database, at the time of downloading of data for initial analyses for the present study, contained more than 20,000 data points/localities (Fig. 6.2). While there is potential for the manner in which data in the database have been collected to distort patterns in the data, and to affect conclusions drawn, it is my view that the large size of the dataset, and its highly diverse data sources over many years (sampled sites mostly since the 1960s), provide some protection from the sort of distortion that could be created by inclusion of data from very large, narrowly-focused, sampling programmes. During the compilation of this paper, the number of sites in the database increased to >26,000 and the full database was used for production of distribution maps.

Some areas of New Zealand, not surprisingly, have less intensive database coverage than others (Fig. 6.2); this variation is due in part to the presence of high mountains where there are no, or few, freshwater habitats and/or to the fact that some sites are difficult to reach. There are also some areas for which there has been little historic interest in sampling or subject to survey, and so data derived from these areas provides much less complete coverage, even though, over the decades represented by the database, some distinctly remote areas have been investigated. This includes Fiordland in the far south west of the South Island where there is a large national park and virtually no road access except for the eastern margins (McDowall 1981; Bonnett and James 1988), and the number of sampling sites is

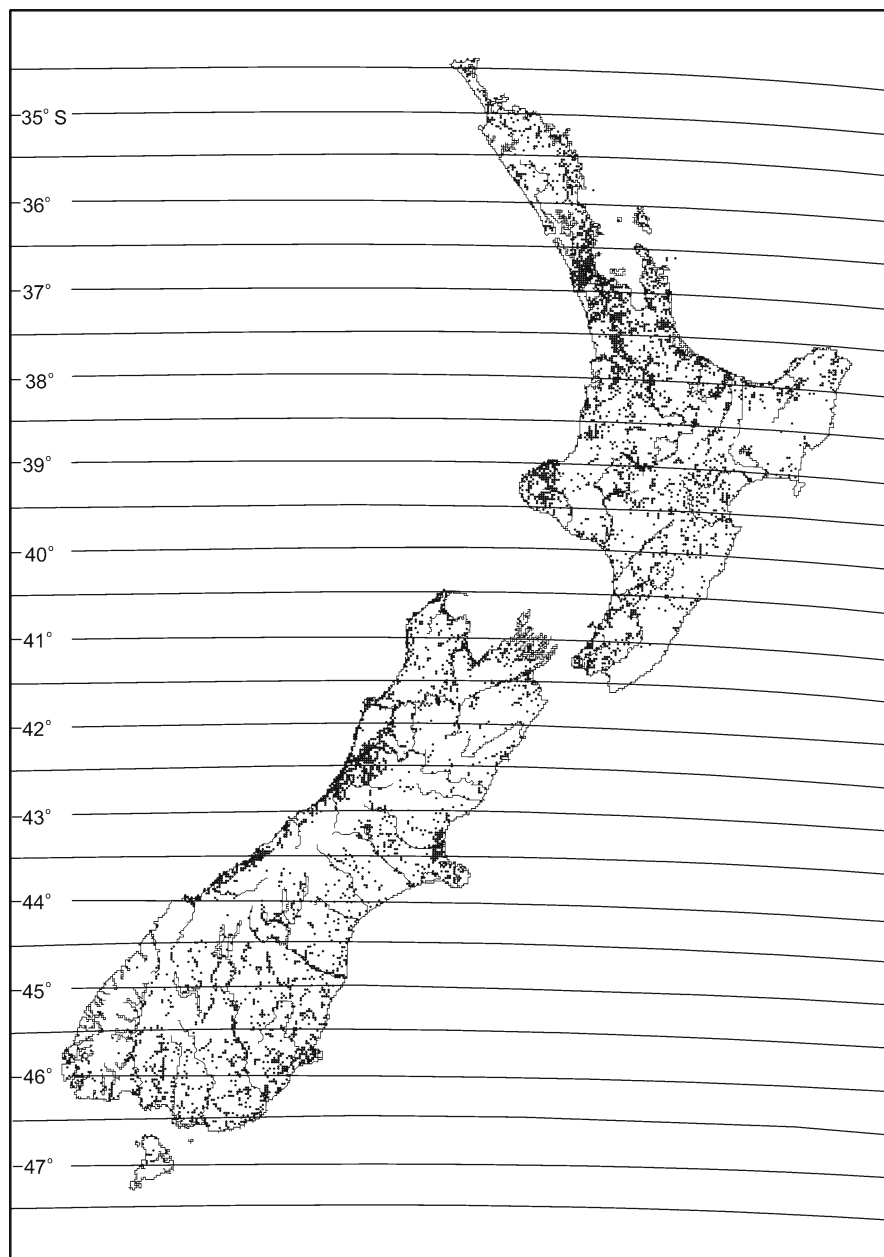


Fig. 6.2 Coverage of New Zealand by the New Zealand freshwater fish database (now, 26,000 data points); superimposed on map are half-degree latitudinal bands across New Zealand

relatively low (see Fig. 10.4). Another little sampled area is Kahurangi National Park in the northwestern South Island (but see Jowett et al. 1998) and again, road access is very limited.

Far southern Stewart Island (see Fig. 2.1) is one of the least explored areas of the country and few sites are represented (see Chadderton and Allibone 2000). And much the same is true of the remote Chatham Islands, well to the east of the main islands of New Zealand (Fig. 2.1) (see Skrzynski 1967; Rutledge 1992). There are also some quite substantial areas of New Zealand where the geology consists of soft, unmetamorphosed sandstones, which make for poor substrates for fish that live in the cover of the stream bed, which is true of much of the fauna. These areas of sandstone tend to have impoverished freshwater fish faunas and have also been neglected for survey and investigation work, historically.

Overall, however, geographic and taxonomic coverage of New Zealand are very substantial and I believe that species' distributions are now well understood; furthermore, recent and continuing additions to the database are generally not radically changing our understanding of the broad patterns of distribution – emerging differences from additional data acquisition are mostly either minor, or largely points of detail. Therefore I think that the data available provide a good perspective on both distribution patterns and fish community associations across the country.

6.3 Data Extraction

Data for the present study were downloaded from the NZFFD and sorted by species, along with associated data for site elevations (= altitude) and distances upstream from the sea as measured along the river channels (= penetration). Data for species in which there are both diadromous and landlocked populations were sorted, and lake-limited populations of these diadromous species were set aside in separate files. This was done because factors influencing elevation and distance inland (or penetration) for landlocked populations may differ from those for diadromous populations. In particular, fish faunas derived from diadromous species, but which represent lacustrine derivatives may be long distances further inland than are attained by the recurring, cohort-scale inland migrations of diadromous conspecifics. This partition of the dataset had to be carried out manually as some individual judgement, based on extensive personal knowledge of the fauna and experience of the river systems, were needed: it could not be done electronically as appropriate criteria are not a part of the database.

Occasionally, diadromous and lacustrine populations (or sub-populations) of a species may share the same lakes or tributaries. In addition, it is known that some diadromous species do not establish landlocked populations (e.g., lamprey, short-jaw kokopu, redfin bully, bluegill bully, giant bully, torrentfish, shortfin and longfin eel), and yet in some instances these species are known to migrate upstream from the sea, through lakes, and into their tributaries that carry landlocked populations of other species. Where this is so, the records from streams above lakes for the

species, just listed, that are known *not* to establish landlocked populations, were included among those species' datasets.

Moreover, the separation of diadromous and lacustrine populations in some species that do establish lacustrine stocks is not always absolutely clear cut – in some instances there is uncertainty about whether populations are diadromous, or not. The number of instances where there was some uncertainty are few, and do not in my view prejudice the interpretation of the broad biogeographical patterns discussed here. When there was some doubt about whether individual lake populations of some species were, or were not, landlocked, such populations were included in the 'landlocked' dataset to ensure that these populations did not distort the elevation/penetration analyses of diadromous stocks. This decision was occasionally somewhat arbitrary.

The database includes figures for elevation and penetration for all sites, and the data on each species' occurrences were stratified into bins covering ranges of 10 m elevation and 10 km penetration. The number of sites represented in each bin typically declines substantially with increase in elevation and penetration. This is largely because the low elevation waterways tend to be sampled more frequently or intensively for a variety of reasons. Partly this is because such sites have easier access. Partly it is because low elevation sites tend to be subject to greater levels of anthropogenic perturbation – water abstraction, polluting discharges, riparian deforestation, impoundment, catchment and channel modification, and so on, so there is a tendency for them to be surveyed more intensively as an aspect of river/habitat/flow management. Because of the variation in the intensity of sampling, when undertaking comparisons of the presence of species across the ranges of elevation and penetration, data on the number of times each species were recorded in each bin were standardised against the number of sites in the lowermost bin for that species. These standardised data were used in plots of elevation/penetration.

6.4 Localities and Place Names

This entire book is structured around the geography of New Zealand, its regions, place names, rivers and lakes, and this poses significant problems for an author wanting to clearly and simply describe the subject regions' geological history, contemporary geography, the patterns of distribution of the taxonomic species involved. Correspondingly, there are difficulties for readers to follow the text, especially, though by no means entirely, for readers wanting to understand the issues. To help deal with these matters, in addition to the general New Zealand localities map (Fig. 2.1) I have provided here a series of maps that have numbered arrows:

- One map shows major river systems (Fig. 6.3).
- Another map shows major lakes (Fig. 6.4).
- And a third focuses on features of rivers and lakes in southern New Zealand (Fig. 6.5), and provides better detail of an area that gets substantial treatment in several parts of the text.

Fig. 6.3 Major rivers dealt with in text: arrowed numbers are explained in gazetteer in this chapter (see p. 142–148)

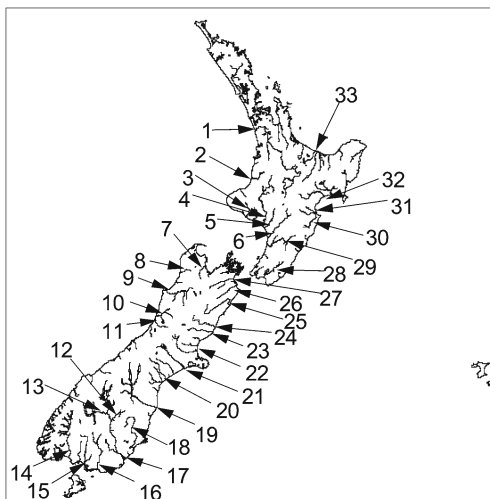
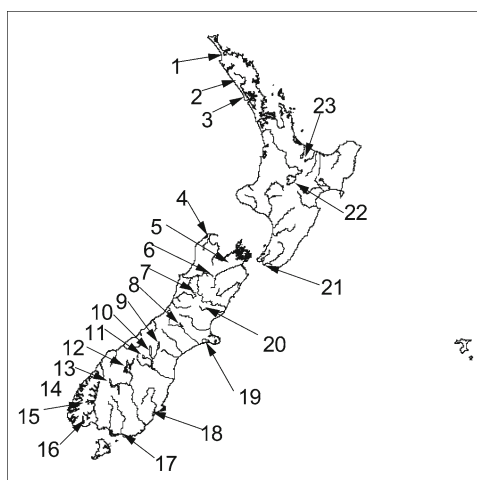


Fig. 6.4 Major lakes dealt with in text: arrowed numbers are explained in gazetteer in this chapter (see p. 142–148)



- A gazetteer (below) provides assistance in connecting the maps and the illustrated features to placenames.

Note that some of the features are so small that it has been impractical to indicate them all on the maps, and there are instance where some features are identified by their proximity to more major features. I am aware that there is some potential for repetition, but concluded that this can be justified as a means of helping to improve clarity.

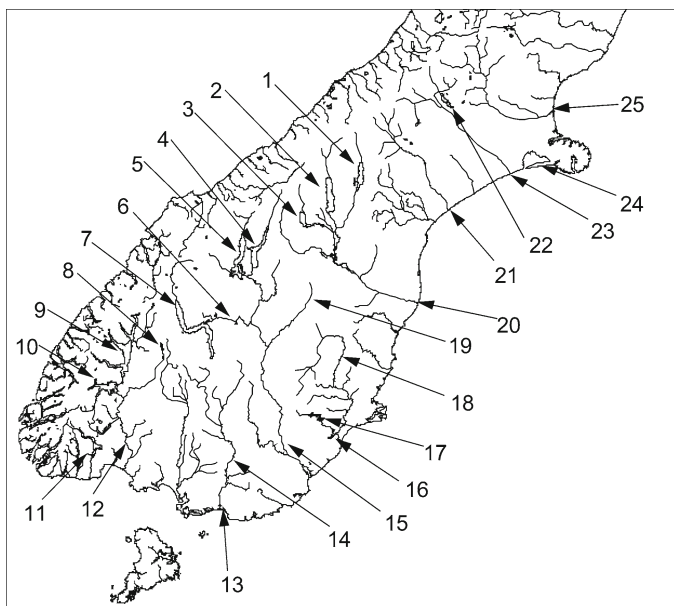


Fig. 6.5 Important water bodies, both rivers and lakes dealt with in text: arrowed numbers are explained in gazetteer in this chapter (see p. 142–148)

There follows, below, a gazetteer of place names that further assists unfamiliar readers in locating names of geographical features of New Zealand. In this gazetteer, all types of geographical features, regions, places, rivers and lakes are listed together. Note that where lakes or rivers are listed below, the name of the feature is given in the form: Taupo, Lake, or Waitaki River.

Abel Tasman National Park An area of coastal reserve land between Tasman Bay (q.v.) to the east and Golden Bay (q.v.) to the west.

Auckland Islands A group of islands c. 465 km south of mainland New Zealand; one of New Zealand's Sub-Antarctic Islands.

Auckland Isthmus A narrow region of northern New Zealand in close proximity to Auckland city (q.v.).

Auckland New Zealand's largest, most northern city.

Aupouri Peninsula The slender tract of land that connects North Cape (q.v.) to the northern end of the North Island.

Awatere River A river draining the Kaikoura Mountains (q.v.) in the northeastern South Island, to the east coast of the Marlborough region (q.v.) in the northeastern South Island; arrow # 26 in Fig. 6.3.

Banks Peninsula A hilly, volcanic peninsula on the east coast of the South Island, associated with the Canterbury region (q.v.).

Bay of Plenty A broad shallow bay, and the land region associated with it, in the northeastern North Island.

- Buller River** A major river that drains from Lakes Rotoiti and Rotoroa (q.v.) west to the northern west coast of the South Island; arrow # 9 in Fig. 6.3.
- Campbell Island** A substantial island c. 700 km south of mainland New Zealand; one of New Zealand's Sub-Antarctic Islands.
- Canterbury Plains** An extended area of flat landscape east of the Southern Alps (q.v.) in the Canterbury (q.v.) region.
- Canterbury** An extended region of the eastern/central South Island, north of the Mackenzie Basin (q.v.).
- Central Otago** An extensive tract of inland landscape of the Otago region (q.v.).
- Chalice, Lake** A small lake in the Wairau River (q.v.) valley in Marlborough (q.v.) in northern South Island; arrow 5 in Fig. 6.4.
- Christabel, Lake** A small lake at the head of the Grey River (q.v.) in the central west coast region of the South Island; arrow 7 in Fig. 6.4.
- Clarence River** A river draining the Kaikoura Mountains (q.v.) in the north-eastern South Island, to the east coast of northern Canterbury (q.v.); arrow 25 in Fig 6.3.
- Clutha River** A major river draining the inland South Island east of the Southern Alps (q.v.) and draining Lakes Wanaka (q.v.) and Hawea (q.v.) in Central Otago (q.v.); arrow 17 in Fig. 6.3; arrow 15 in Fig. 6.5.
- Coleridge, Lake** A glacial lake at the head of the Rakaia River (q.v.) in Canterbury (q.v.); arrow 8 in Fig. 6.4; arrow 22 in Fig. 6.5.
- Cook Strait** The sea strait between the North and South Islands.
- Coromandel Peninsula** A slender peninsula of land east of Auckland (q.v.).
- Dunedin** A major, coastal city in southeastern South Island.
- East Cape** The far northeastern extremity of the North Island, east of Bay of Plenty (q.v.).
- Ellesmere, Lake** A low elevation, coastal, tidal brackish lake in Canterbury (q.v.) just south of Banks Peninsula (q.v.); arrow 19 in Fig. 6.4; arrow 24 in Fig. 6.5.
- Farewell Spit** An extended strip of coastal sand at the northwestern extremity of the South Island.
- Fiordland** An area of landscape at the southwestern extremity of the South Island.
- Foveaux Strait** A sea strait between the southern South Island and Stewart Island (q.v.).
- Gisborne** A city in Poverty Bay (q.v.), in the eastern North Island.
- Golden Bay** A deep bay at the northwestern extremity of the South Island, just west of Tasman Bay (q.v.).
- Great Barrier Island** A small island in eastern northern New Zealand, east of Auckland (q.v.).
- Grey River** A river that drains from the western flanks of the Southern Alps (q.v.) in the northern west coast of the South Island; a little south of the Buller River (q.v.); arrow 10 in Fig. 6.3.
- Hauraki Plains** An area of low-lying land south of Coromandel Peninsula (q.v.).

- Hauroko, Lake** A glacial lake in eastern Fiordland (q.v.) that drains to sea via the Wairaurahiri River in the southern South Island; arrow 16 in Fig. 6.4; arrow 11 in Fig. 6.5.
- Hawea, Lake** A major glacial lake in Central Otago (q.v.) that drains to the east through the Clutha River (q.v.); arrow 12 in Fig. 6.4, same number also indicates Lake Wanaka (q.v.); arrow 4 in Fig. 6.5.
- Hawkes Bay** A deep bay and the land region associated with it in the central/eastern North Island.
- Heaphy River** River that flow west in far northern South Island.
- Hokitika River** A river that drains the western flanks of the Southern Alps (q.v.) in the northern/central west coast of the South Island, south of the Grey River (q.v.); arrow 11 in Fig. 6.3.
- Hurunui River** A river draining to the east coast from the eastern flanks of the Southern Alps (q.v.) in northern Canterbury (q.v.) in the eastern South Island; arrow 23 in Fig. 6.3.
- Kahurangi National Park** A large area of reserve land near the northwestern end of the South Island.
- Kai Iwi Lakes** A group of small lakes in western Northland; arrow 2 in Fig. 6.4.
- Kaihoka Lakes** Two small lakes near Whanganui Inlet in northwestern South Island; arrow 4 in Fig. 6.4.
- Kaikoura Mountains** Mountain ranges that are somewhat to the east of the main northern end of the Southern Alps (q.v.) and in close proximity to the east coast of the South Island.
- Kaimanawa Ranges** A mountain range of inland Hawkes Bay (q.v.) in the eastern/central North Island.
- Kapiti Island** A small island offshore in the Wellington region (q.v.).
- Kawarau River** An inland tributary of the Clutha River (q.v.) that drains Lake Wakatipu (q.v.); arrow 6 in Fig. 6.5.
- Little Barrier Island** A small island near Great Barrier Island (q.v.) east of Auckland (q.v.) in the eastern/northern New Zealand.
- Mackenzie Basin** An extended inland region of the southeastern South Island, lying between Canterbury (q.v.) in the north and Otago (q.v.) in the south; includes the headwaters and headwater lakes of the Waitaki River (q.v.).
- Manapouri, Lake** A major glacial lake in eastern Fiordland, in the southern South Island that drains to the south to sea via the Waiau River (q.v.); arrow 15 in Fig. 6.4; arrow 10 in Fig. 6.5.
- Manawatu Gorge** A river-cut channel between the Tararua (q.v.) and Ruahine (q.v.) ranges, by the Manawatu River (q.v.).
- Manawatu River** A river that drains the eastern flanks of the Tararua (q.v.) and Ruahine (q.v.) Ranges of the southern North Island, and then cuts a gorge between these mountain ranges, and then west to the west coast of the southern North Island; arrow 29 in Fig. 6.3.
- Maniototo** An area of inland, eastern Otago, drained by the Taieri River (q.v.).
- Manuherikia River** A major inland (northern) tributary of the Clutha River (q.v.); arrow 12 in Fig. 6.3; arrow 19 in Fig. 6.5.

- Marlborough** The northeastern region at the tip of the South Island; the Marlborough Sounds are an area of deeply indented coastline, the land major feature of Marlborough.
- Mataura River** A river draining the Southland Plains (q.v.) to the south coast of the South Island; arrow 16 in Fig. 6.3; arrow 14 in Fig. 6.5.
- Mavora Lakes** Small, glacial lakes at the head of the Waiau River, arrow 8 in Fig. 6.5.
- Mohaka River** A river draining the eastern flanks of the Kaimanawa Ranges (q.v.) of the eastern/central North Island, draining to the east, to the sea in Hawkes Bay (q.v.); arrow 32 in Fig. 6.3.
- Mokau River** A river draining to the west coast north of the Taranaki region (q.v.); arrow 2, in Fig. 6.3.
- Nelson** A city and also the region at the northwestern end of the South Island.
- Ngaruahoe, Mount** One of three closely-sited semi-active volcano in the central North Island.
- Ngaruroro River** A river draining the eastern flanks of the Kaimanawa Ranges (q.v.) in inland Hawkes Bay (q.v.); arrow 31 in Fig. 6.3.
- North Cape** The far northern extremity of New Zealand.
- Northland** A slender peninsula forming the most northern region of New Zealand.
- Ohau, Lake** A major glacial lake in the Mackenzie Basin (q.v.) draining into the Ohau River, at the head of the Waitaki River (q.v.); arrow 11 in Fig. 6.4; arrow 3 in Fig. 6.5.
- Onoke, Lake** A shallow, estuarine coastal lake in the southern North Island; arrow 21 in Fig. 6.4; # also provides position of Lake Wairarapa (q.v.).
- Oreti River** A river draining the Southland Plains (q.v.) to the south coast of the South Island; arrow 15 in Fig. 6.3.
- Otago Peninsula** A small, hilly, volcanic peninsula at the eastern fringes of the Otago region (q.v.) and in close proximity to Dunedin city (q.v.).
- Otago** A substantial region of the southeastern South Island, north of Southland (q.v.).
- Ototoa, Lake** A small lake on the south head of the Kaipara Harbour in western Northland (q.v.); not shown on map, but a little south of arrow 3 in Fig. 6.4.
- Patea River** A river that drains the eastern slopes of Mount Taranaki (q.v.), south through the Taranaki region (q.v.) to the west coast of the North Island; arrow 3 in Fig. 6.3.
- Poutu Lakes** A group of small lakes on the north head of the Kaipara Harbour in western Northland (q.v.); arrow 3 in Fig. 6.4.
- Poverty Bay** A small bay and the associated land region south of East Cape (q.v.).
- Pukaki, Lake** A major glacial lake in the Mackenzie Basin (q.v.) draining into the Pukaki River, at the head of the Waitaki River (q.v.); arrow 10 in Fig. 6.4; arrow 2 in Fig. 6.5.
- Rakaia River** A major river that drains the eastern flanks of the Southern Alps (q.v.) to the east coast of central Canterbury (q.v.) in the eastern South

Island, south of Banks Peninsula (q.v.); arrow 21 in Fig. 6.3; arrow 23 in Fig. 6.5.

Rangitaiki River A river of the inland northeastern North Island, draining northwards to sea in the eastern Bay of Plenty (q.v.); arrow 33 in Fig. 6.3.

Rangitata River A river that drains the eastern flanks of the Southern Alps (q.v.) to the east coast of central Canterbury (q.v.) in the eastern South Island; arrow 20 in Fig. 6.3; arrow 21 in Fig. 6.5.

Rangitikei River A major river draining the central North Island, south to the west coast of the North Island, a little southeast of the Turakina (q.v.) and Whangaehu (q.v.) Rivers; arrow 6 in Fig. 6.3.

Rotoiti, Lake A glacial lake at the head of the Buller River (q.v.) in the inland northern South Island; Lake Rotorua is at same arrow: arrow 6 in Fig. 6.4. NB: there is another lake of the same name in the Rotorua lakes (q.v.) of the northern/central North Island, near arrow 23 in Fig. 6.4.

Rotorua, Lake A glacial lake at the head of the Buller River (q.v.) in the inland northern South Island; Lake Rotoiti is at same arrow: arrow 6 in Fig. 6.4.

Rotorua Lakes A group of numerous lakes, including one known as Lake Rotorua in inland Bay of Plenty (q.v.) that drain to sea in the bay of that name; arrow 23 in Fig. 6.4.

Ruahine Ranges A major mountain range that runs north/south in the southern/central North Island, north of the Manawatu Gorge (q.v.) and the Tararua (q.v.) Ranges.

Ruamahanga River A river that drains the eastern flanks of the Rimutaka Ranges, to the south coast of the North Island, running to sea through Lake Onoke (q.v.); arrow 28 in Fig. 6.3.

Ruapehu, Mount One of three closely-sited semi-active volcanoes in the central North Island.

Selwyn River A river draining the Canterbury Plains (q.v.) into Lake Ellesmere (q.v.) just south of Banks Peninsula (q.v.).

Southern Alps The major mountainous landscape feature of the South Island; the alps trend northeast/southwest, slightly oblique to the South Island itself.

Southland Plains An area of flat land across the southern South Island.

Southland The southernmost region of New Zealand.

Stewart Island A substantial southern island of New Zealand.

Sumner, Lake Lake at the head of the Hurunui River (q.v.) in northern Canterbury (q.v.); arrow 20 in Fig. 6.4.

Taieri River A river draining east and south from the Maniototo Plains in inland, eastern Otago (q.v.); arrow 18 in Fig. 6.3; arrow 18 in Fig. 6.5.

Takaka River River that flows north into Golden Bay (q.v.) in the northern South Island; arrow 7 in Fig. 6.3.

Taramakau River A river that drains the western flanks of the Southern Alps (q.v.) in the northern/central west coast of the South Island, south of the Grey River (q.v.); is not shown in Fig. 6.3 owing to very close proximity to (north of) the Hokitika River (q.v.) at arrow 11 in Fig. 6.3.

- Taranaki, Mount** A substantial, largely quiescent volcano in the Taranaki region (q.v.).
- Taranaki** A land region in the western/central North Island, south of the Waikato (q.v.).
- Tararua Ranges** A major mountain range that runs north/south in the southern North Island, south of the Manawatu Gorge (q.v.) and the Ruahine (q.v.) Ranges.
- Tasman Bay** A deep bay at the northern extremity of the South Island, near Nelson (q.v.).
- Taupo, Lake** New Zealand's largest lake in the central North Island that drains north and then west to sea via the Waikato River (q.v.); arrow 22 in Fig. 6.4.
- Te Anau, Lake** A major glacial lake in eastern Fiordland, in the southern South Island that drains to the south to sea via the Waiau River (q.v.) and Lake Manapouri (q.v.); arrow 14 in Fig. 6.4; arrow 9 in Fig. 6.5.
- Tekapo, Lake** A major glacial lake in the Mackenzie Basin (q.v.) draining into the Tekapo River, at the head of the Waitaki River (q.v.); arrow 9 in Fig. 6.4; arrow 1 in Fig. 6.5.
- Tokerau Lagoon** A small lake in eastern Northland (q.v.); not shown but at # 1 in Fig. 6.4.
- Tongariro, Mount** One of three closely-sited semi-active volcanoes in the central North Island.
- Tukituki River** A river draining the eastern flanks of the Ruahine Ranges (q.v.) into southern Hawkes Bay (q.v.); arrow 30 in Fig. 6.3.
- Waiau River** A river that drains Lakes Te Anau (q.v.) and Manapouri (q.v.) to the southern coast of the South Island in eastern Fiordland (q.v.); arrow 14 in Fig. 6.3; arrow 12 in Fig. 6.5.
- Waiau-ua River** A river draining to the east coast from the eastern flanks of the Southern Alps (q.v.) in northern Canterbury (q.v.) in the eastern South Island; arrow 24 in Fig. 6.3.
- Waihola, Lake** A low elevation lake on the Waipori River in coastal Otago (q.v.) on the Taieri River (q.v.); arrow 18 in Fig. 6.4 ; # also signifies Lake Waipori; arrow 17 in Fig. 6.5.
- Waikato River** A major river that drains from Lake Taupo (q.v.) north through the central North Island, and then west to the coast, in the Waikato region (q.v.); arrow 1, in Fig. 6.3.
- Waikato** A land region south of Auckland (q.v.) through which the Waikato River flows.
- Waimakariri River** A major river that drains the eastern flanks of the Southern Alps (q.v.) to the east coast of central Canterbury (q.v.) in the eastern South Island, north of Banks Peninsula (q.v.); arrow 22 in Fig. 6.3; arrow 25 in Fig. 6.5.
- Waipori, Lake** A low elevation lake on the Waipori River in coastal Otago (q.v.) on the Taieri River (q.v.); arrow 18 in Fig. 6.4 ; arrow 16 in Fig. 6.5; # also signifies Lake Waihola.

- Wairarapa, Lake** A shallow lowland lake in the southern North Island that drains to sea via Lake Onoke (q.v.); arrow 21 in Fig. 6.4; # also signifies Lake Onoke (q.v.).
- Wairarapa** A region in the southeastern North Island, east of Wellington (q.v.).
- Wairau River** A river draining the Kaikoura Mountains (q.v.) in the northern South Island, to the northern coast of Marlborough (q.v.) in the northern South Island; arrow 27 in Fig. 6.3.
- Wairaurahiri River** Drains from Lake Hauroko in southern Fiordland; arrow 11 in Fig. 6.5.
- Waitaki River** A major river of the eastern central Southern Alps (q.v.) of the South Island, that drains the Mackenzie Basin (q.v.), flows east and derives from a series of inland lakes, Tekapo (q.v.), Pukaki (q.v.) and Ohau (q.v.) in the Mackenzie Basin; arrow 19 in Fig. 6.3; arrow 20 in Fig. 6.5.
- Waituna Lagoon** A shallow lowland lake near the mouth of the Maituna River (q.v.) in Southland (q.v.) in the southern South Island; arrow 17 in Fig. 6.4; arrow 13 in Fig. 6.5.
- Wakatipu, Lake** A major glacial lake in Central Otago (q.v.) that drains to the east through the Kawarau River (q.v.) and then Clutha River (q.v.); arrow 13 in Fig. 6.4; arrow 7 in Fig. 6.5.
- Wanaka, Lake** A major glacial lake in Central Otago (q.v.) that drains to the east through the Clutha River (q.v.); arrow 12 in Fig. 6.4, same number also indicates Lake Hawea (q.v.) arrow 5 in Fig. 6.5.
- Wellington** Both the southeastern region of the North Island and a city at the southern tip of the North Island.
- Westland** An extended region of the western South Island, west of the Southern Alps (q.v.).
- Whangaehu River** A river draining the central North Island to the southwestern coast of the North Island, a little south of the Whanganui River (q.v.); arrow 5 in Fig. 6.3.
- Whanganui River** A major river draining from the central North Island, in part from the central North Island volcanoes, to the west coast of the North Island, south of Taranaki; arrow 4 in Fig. 6.3.

References

- Bonnett ML, James GD (1988) Freshwater fish in Preservation and Chalky Inlets. *Freshwater Catch* (N Z) 34:12–14
- Chadderton WL, Allibone RM (2000) Habitat use and longitudinal distribution patterns of native fish from a near pristine Stewart Island stream. *N Z J Mar Freshwater Res* 34:487–499
- Jowett IG, Hayes JW, Deans N, Eldon GA (1998) Comparisons of fish communities and abundance in unmodified Kahurangi National Park with other areas of New Zealand. *N Z J Mar Freshwater Res* 32:307–322
- Ling N, Gleeson DM (2001) A new species of mudfish, *Neochanna* (Teleostei: Galaxiidae) from northern New Zealand. *J R Soc N Z* 31:385–392

- McDowall RM (1981) Freshwater fish in Fiordland National Park. N Z Min Agric Fish, Fish Environ Rep 12:1–31
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Reed, Auckland, 551 pp
- McDowall RM (2000) The Reed guide to New Zealand freshwater fishes. Reed, Auckland, 224 pp
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). J R Soc N Z 34:315–331
- McDowall RM (2006) The taxonomic status, distribution and identification of the *Galaxias vulgaris* species complex in the eastern South Island and Stewart Island. NIWA Client Rep CHCDOC2006-081:1–40
- McDowall RM, Chadderton WL (1999) *Galaxias gollumoides* (Teleostei: Galaxiidae) from Stewart Island, with notes on other non-migratory fishes present on the island. J R Soc N Z 29:77–88
- McDowall RM, Hewitt J (2004) Attempts to distinguish morphotypes in the Canterbury-Otago non-migratory *Galaxias* species complex. N Z Dep Conserv Sci Int Ser 165:1–18
- McDowall RM, Richardson J (1984) New Zealand freshwater fish survey: a guide to input and output. N Z Min Agric Fisher, Fish Info Leaf 12:1–15
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. N Z J Zool 29:41–52
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. J R Soc N Z 33:675–691
- Mitchell CP (1995) A new species of *Galaxias* (Pisces: Galaxiidae) from the Chatham Islands, New Zealand. J R Soc N Z 25:89–93
- Richardson J (2005) New Zealand freshwater fish database user guide. NIWA Client Rep HAM2005-033:1–28
- Rutledge MJ (1992) Survey of Chatham Island indigenous freshwater fish, November 1989. Department of Conservation, Christchurch, N Z, 18 pp
- Skrzynski W (1967) Freshwater fishes of the Chatham Islands. N Z J Mar Freshwater Res 1:89–98

Chapter 7

Phylogenetic Lineages in the Fauna and the Evolution of Diadromy: A Broad Perspective

Abstract Seven fish families are represented in the New Zealand freshwater fish fauna: Geotriidae, Retropinnidae, and Galaxiidae are families of southern cool-temperate affiliations and origins, whereas Anguillidae, Pinguipedidae, Eleotridae, are Pleuronectidae groups of Indo-West Pacific derivations. More than half the species are Galaxiidae, with Eleotridae of second importance. About half the species are diadromous, and the non-diadromous species are regarded as derived from diadromous one through the abandonment of migrations to and from the sea.

Keywords Anguillidae • Diadromy • Eleotridae • Galaxiidae • Geotriidae • Landlocking • Pinguipedidae • Pleuronectidae • Retropinnidae • Relationships

7.1 Phylogenetic Relationships in the Fauna

At one spatial scale, the biogeography of New Zealand's freshwater fish fauna is about how that fauna is related to those in other lands, and issues relating to these relationships are introduced in the present chapter. Logically, we might expect that these relationships would involve other southern lands, especially Australia, given its relatively close geographical proximity to New Zealand and also the fact that New Zealand and Australia were once both a part of the great, ancient southern continent Gondwana (see [Fig. 3.1](#)) – Australia is certainly the nearest major land area. If we were to inform our search for connections for the freshwater fish fauna by looking at the relationships of other groups of animals and plants present in New Zealand, we would certainly tend to look at what lives in Australia, perhaps also New Caledonia, and probably even more broadly in Patagonian South America and southern Africa. Our knowledge of other, iconic, New Zealand animal and plant groups, such as the ratite birds (moa, kiwi – Cooper et al. 1992; Haddrath and Baker 2001; Baker et al. 2005), southern beeches trees (genus *Nothofagus* – Swenson et al. 2001; Knapp et al. 2005; Cook and Crisp 2005), perhaps other forest trees such as podocarps (f. Podocarpaceae: rimu, kahikatea)

and araucarians (kauri – Stockler et al. 2002; Knapp et al. 2007) or the chironomid midges (small aquatic flies – Brundin 1965, 1966), would point substantially to the broad, cold-temperate southern distributions of such groups, and plenty more groups could be named. In broad and general terms, the relationships of most of New Zealand's animals and plants are in Australia (Winkworth et al. 2005; McGlone 2005, 2006; Gibbs 2006; Wallis and Trewick 2009), and biotic connections there remain very strong, with many species of birds and plants, especially, shared to the west across the Tasman Sea to Australia and north to New Caledonia. Others connect to Patagonian South America, and even more widely, with some elements having relationships as far away as temperate lands of the Northern Hemisphere. Equally, if we were to be guided by our knowledge of where else such families as the galaxiid fishes are known to live, much the same group of southern lands would tend to come to mind.

Knowing about the phylogenetic relationships among New Zealand's freshwater fishes, and about their relationships to other groups and geographical areas, over a broad geographical span, is important to understanding the way the fauna has become distributed among, and adapted to, New Zealand's fresh waters and what these adaptations mean in a broad phylogenetic and biogeographical context (Wiens and O'Donoghue 2004). Diadromy proves to be a key element in determining all manner of aspects of the fauna's distribution, as well as of the structuring of freshwater fish communities that they form (Hayes et al. 1989; McDowall 1993, 1996a, b, 1998; McDowall and Taylor 2000; Joy and Death 2000, 2002; Eikaas et al. 2005, 2006; Eikaas and McIntosh 2006; Leathwick et al. 2005, 2008; and see Chapter 5: Some essentials of freshwater fish biogeography). This makes it important to know whether the wide presence of diadromy represents a useful, novel, local adaptation, or whether so many species are diadromous simply, or at least in part, because they share a common diadromous ancestry with fish elsewhere (Harvey 1996; Brooks 1985; Brooks and McLennan 2001, 2002). Presumably, diadromy might have been lost if it did not convey significant adaptive advantages, though it might not simply be a question of adaptation. It is also possible that, at least in some groups, diadromy is a physiological imperative – migrations between fresh water and the sea may be critical to the survival of some life stages.

At present we can only speculate about these interesting proximate (osmoregulatory) and ultimate (evolutionary) questions. However, some hints as to the importance of diadromy for anguillid eels can be derived from the observation that all anguillids, worldwide, spawn in the sea (Tesch 2003).

The details of the biogeographical history of the galaxiids, in particular, have been of great past interest in biogeography. Because of the family's very broad southern range, its biogeography has been the subject of substantial controversy for over a century and a half. This important, almost pivotal, question is discussed in some detail in the next chapter. Meanwhile, I want here to look at distribution patterns a little more generally, and as I do, several distinct patterns present themselves.

7.2 Family Geotriidae

The southern pouched lamprey, family Geotriidae, contains but a single species, *Geotria australis* (Fig. 7.1), which is known from southwestern and southeastern Australia, Tasmania, and Patagonian South America (Hubbs and Potter 1986; McDowall 1990), a distribution that is very similar to that of the inanga (Fig. 7.2). An old record of *Geotria* from the Falkland Islands (Gorham 1977) is questionable as it has never been repeated, and the species was not found there in recent surveys

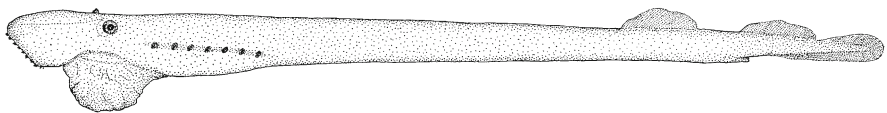


Fig. 7.1 Southern pouched lamprey, *Geotria australis* 465 mm TL (family Geotriidae)

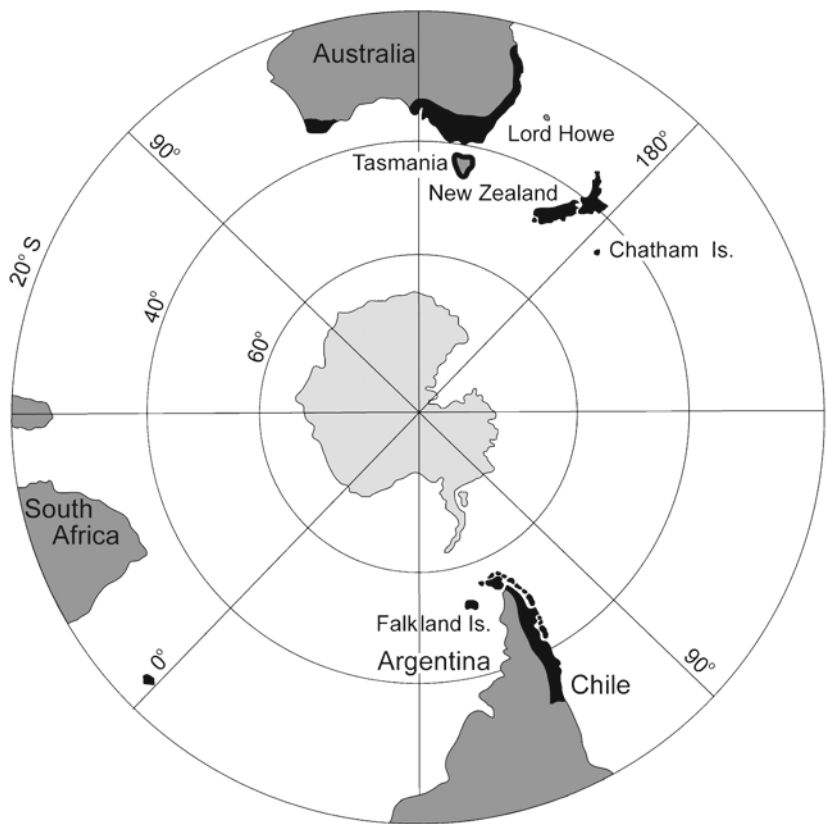


Fig. 7.2 Very broad southern cold-temperate distribution of *Galaxias maculatus* (family Galaxiidae)

of the islands' fresh waters (McDowall et al. 2001, 2005; Ross 2009). There is a companion Southern Hemisphere lamprey family Mordaciidae, which is found in Australia and Patagonian South America (but not New Zealand), and these two southern lamprey families together form a sister clade to the entire Northern Hemisphere, cool temperate lamprey family Petromyzontidae. So here we are seeing a largely southern cool-temperate group that is part of a southern/northern bipolar pair at moderate to high, latitudes in both hemispheres. Diadromy is a very widespread life history strategy across the diversity of lampreys, generally (Hubbs and Potter 1986; McDowall 1988; Gill et al. 2003), and has the appearance of an ancestral character in lampreys as a whole.

Geotria is anadromous, and no landlocked/freshwater-restricted populations are known; nor are there entirely fluvial sister taxa like there are in the other southern lamprey genus *Mordacia*, or in some of the Northern Hemisphere lampreys (Hubbs and Potter 1986; Potter 1996). *Geotria* seems certain to have taken its diadromy with it as (and however), it became very widespread around the cool-temperate Southern Hemisphere. There is every reason to think that *Geotria* has spread widely through the sea to achieve its present very broad geographical range, and it is known from the seas around Patagonian South America primarily through its involvement in the diets of ocean-wandering and feeding albatrosses there (Potter et al. 1979). The two families of southern lampreys are clearly of southern cool-temperate provenance.

7.3 Family Anguillidae

New Zealand has three anguillid eels, of which only the longfin, *Anguilla dieffenbachii*, is endemic; the shortfin and spotted eels (*A. australis* and *A. reinhardtii*) are shared with southeastern Australia as well as some islands of the western subtropical Pacific Ocean. All anguillid eels, including those in New Zealand, are diadromous (catadromous – McDowall 1988; Tesch 2003).

As noted above all freshwater eels are diadromous and diadromy has certainly arrived at least twice in New Zealand as eels first invaded the country's fresh waters. The spotted eel (Fig. 7.3) appears to have arrived in New Zealand very recently (Jellyman et al. 1996; McDowall et al. 1998) though, as noted earlier (Chapter 1), there is a somewhat uncertain, earlier New Zealand record of this species in the 1920s (Phillipps 1925), which raises the prospect that there may have been an earlier episode of this species being present in New Zealand, or even the possibility that there has long been variable, occasional, perhaps even episodic recruitment of this species to New Zealand. The phylogenetic



Fig. 7.3 Spotted eel *Anguilla reinhardtii*, 480 mm TL (family Anguillidae): a relatively recent arrival in New Zealand fresh waters, probably

relationships of the endemic longfin may be with the New Zealand shortfin (Tsukamoto and Aoyama 1998; Tsukamoto et al. 2002; Aoyama 2003); whether or not that is so, it is evident that at least some of the anguillid biodiversity in New Zealand has evolved locally. Diadromy is retained in all populations of all three species. Pertinent to this is the fact that nowhere, globally, have anguillid eels been able to establish freshwater-limited (landlocked) populations – reproduction is locked absolutely into marine migration, spawning and egg development in *Anguilla* (McDowall 1988; Tesch 2003), as it is in the entire Order Anguilliformes; and it is not known whether diadromy is a physiological imperative for the genus *Anguilla* as a whole.

There is, however, growing evidence that some individual eels may fail to enter fresh water, but may instead spend their whole lives in coastal, perhaps sometimes brackish, seas (Tsukamoto and Nakae 1998; Tsukamoto and Aoyama 1998; Tsukamoto et al. 2002; McCleave and Edeline 2009). It is possible that the marine spawning, development, and early larval life of anguillid eels are physiological/behavioural imperatives – that they cannot be achieved in fresh water for physiological reasons, rather than being specific local attributes that are informative about the adaptive advantages of diadromy in such eels.

The whole question of the vast migratory distances that anguillid eels swim to reach their spawning grounds, and what controls/guides their migrations, remains poorly investigated and little understood, but much the best known for the two Atlantic species of *Anguilla* (Bertin 1956; Tesch 2003; den Thillart et al. 2009), but is beginning to be understood for New Zealand anguillids (Jellyman and Bowen 2009). Much remains to be learned.

The genus *Anguilla* is widespread through much of the tropical and subtropical oceans/lands of the world (absent from the eastern Pacific). The 16 species of *Anguilla* (Tesch 2003) probably need to be seen as having their origins in the warmer regions of the global oceans, and the group very much achieves its southernmost geographical limits in southern New Zealand at around latitude 48°S. New Zealand's eels can thus be viewed as a cold-temperate range extension of a substantially warm temperate to tropical 'Indo-Pacific' taxon.

7.4 Family Retropinnidae

The now extinct New Zealand grayling, *Prototroctes oxyrhynchus* (see Fig. 1.3), is believed to have been diadromous (amphidromous), and is one of two congeneric species, the other species, *P. maraena*, also diadromous, being in southeastern Australia and Tasmania (McDowall 1996c). Thus, *Prototroctes* is an Australasian (Australia+New Zealand) genus and its diadromy is not a distinctive adaptation for the New Zealand fauna (the Australian species could, of course, be derived from the New Zealand one and its diadromy originated there, or the reverse, and this cannot be discounted – and is unlikely to be resolved). Regardless, diadromy is a seemingly mandatory feature of the genus *Prototroctes* as a whole. Hector (1872) referred to “very large fish called trout, which are sometimes cast upon the shores of the great

inland lakes of Otago”, that he thought belonged to this species. He mentions fish of “6–8 pounds”. However, the sources and authenticity of these reports are unclear, and it is certain that no other records of the New Zealand grayling that were anywhere near as large as this, one weighing a kilogram being very large (McDowall 1990).

There is no explicit evidence that *Prototroctes* was ever landlocked in New Zealand, and there are no lake-limited populations of the Australian species (McDowall 1996c). As with anguillid eels, diadromy could be a physiological imperative for the southern graylings, as there is no hint that either species has been able to abandon larval and juvenile life at sea, and become entirely freshwater-dwelling.

New Zealand has two endemic species of retropinnine smelts: one species in the more widespread genus *Retropinna* (in which there are also two species, one each in southeastern Australia and Tasmania), plus New Zealand’s endemic monotypic *Stokellia* (McDowall 1979). Both New Zealand species are diadromous (anadromous), as is the Tasmanian smelt, *R. tasmanica*, and there is some, growing, evidence that the mainland Australian *R. semoni* may also sometimes be anadromous (Crook et al. 2008), though that species is clearly highly facultative. Whether *Stokellia* shares a closest common ancestry with New Zealand *Retropinna* is uncertain but it seems likely, simply on geographical grounds.

Diadromy in New Zealand’s common smelt is highly facultative, with many independently-derived landlocked populations, some of them established by historical human translocations of fish of diadromous provenance (McDowall 1990, 2002b). However, *Stokellia* is always anadromous and there are no known lake populations. Again, determining whether diadromy evolved or arrived in New Zealand with *Retropinna* seems unlikely to be easy, and probably is of little biogeographical importance.

7.5 Family Galaxiidae

The question of the biogeography of the quite speciose Galaxiidae has long been a matter of intense interest, and is dealt with in detail in the next chapter (Chapter 8: *Galaxias* and Gondwana). However, there are some issues relating to phylogenetic relationships and the presence of diadromy among galaxiids that are better discussed in the present chapter. In brief, galaxiids are a very widespread, southern, largely cool- to cold-temperate, group that is known from Australia, New Caledonia, Lord Howe Island, New Zealand, the Chatham, Auckland and Campbell Islands, Patagonian South America, the Falkland Islands, and southern Africa (see Fig. 8.1) – thus, they certainly look very ‘southern’ and appear Gondwanan in range (discussed in much more detail in Chapter 8). An Indian galaxiid (Day 1888) has long been discounted (McDowall 1973a).

Among the New Zealand galaxiids there are five diadromous *Galaxias* species and, of these, two are conspecific with populations in southeastern Australian/Tasmanian species (koaro, *Gl. brevipinnis*, and inanga, *Gl. maculatus*: McDowall and Fulton 1996), the latter also being found to the east in Patagonian South America and the Falkland Islands (McDowall 2002a) (Fig. 7.2). The derivations of

the other three diadromous New Zealand *Galaxias* species are less clear, but they may, together, form the sister-group of additional, diadromous, southeastern Australian/Tasmanian galaxiids (McDowall 1970).

In addition, though none of New Zealand's five species of *Neochanna* mudfishes is diadromous, they share a common ancestry with the Tasmanian/Victorian mudfish, *Neochanna cleaveri* (Fig. 7.4) (McDowall and Fulton 1996; McDowall 1997;

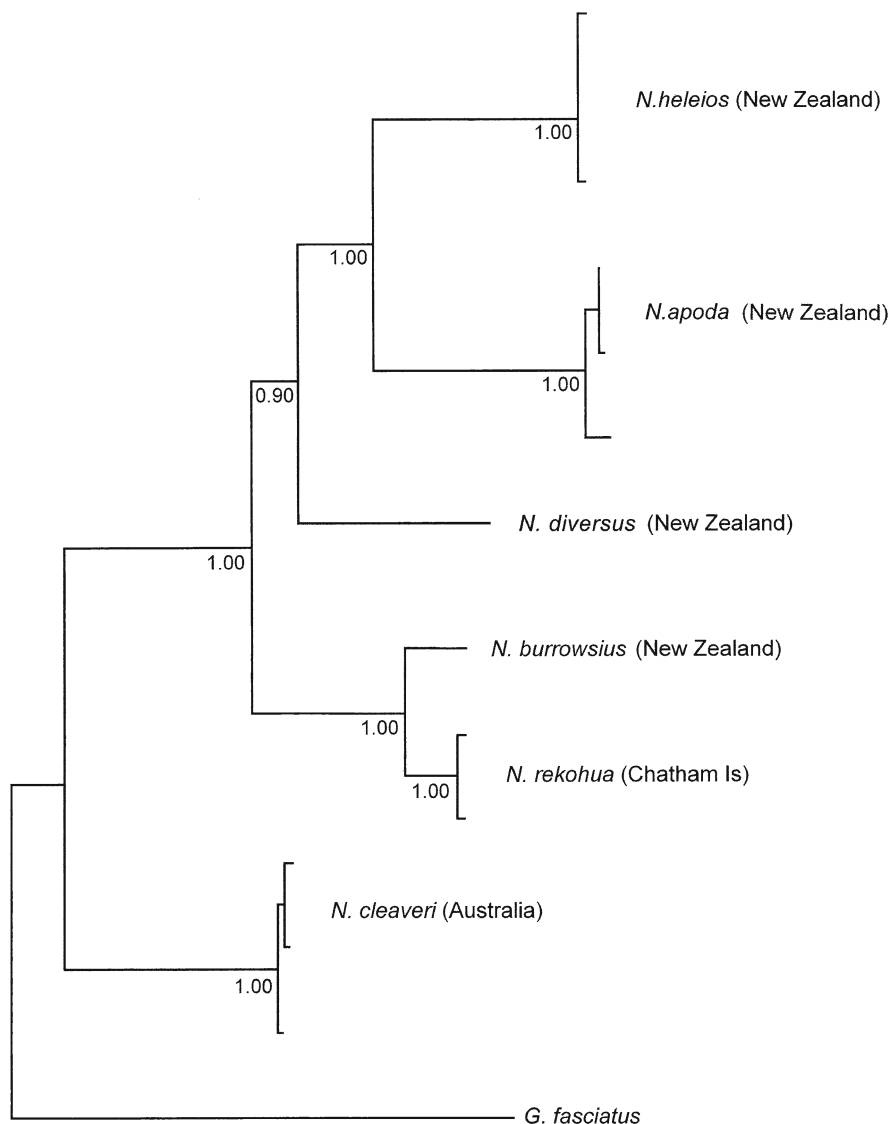


Fig. 7.4 Hypothesised relationships among the *Neochanna* mudfishes in Australia and New Zealand – a total evidence phylogeny derived from Bayesian analysis of combine cytochrome *b* (1160 base pairs) 16S rRNA (521 base pairs) and morphology (21 characters); posterior probability values ≥ 0.90 are indicated with associated nodes (adapted from Waters and McDowall, 2005)

Waters and White 1997; McDowall 2004b; Waters and McDowall 2005), which is diadromous (amphidromous – Fulton 1986); thus *Neochanna* clearly represents an additional Australian-New Zealand biotic/phylogenetic linkage. The Australian species has a marine-living whitebait juvenile that is substantially smaller than the whitebait juveniles of the amphidromous *Galaxias* species (c. 30 mm long, compared with 45–55 mm in the whitebait *Galaxias* (McDowall 1984; Fulton 1986). Diadromy in *Neochanna* prompts the conclusion that *Neochanna* reached New Zealand from Australia by transoceanic dispersal, with diadromy being lost in the New Zealand members of the genus. Some further aspects of this question are addressed in Chapter 14.

To summarise, there are at least three, perhaps four, distinct galaxiid lineages in New Zealand that share ancestries with Australian diadromous species or lineages to the west; and one of these connections (inanga) also extends eastwards across the southern Pacific Ocean, to Patagonian South America and the Falkland Islands (Fig. 7.2) (McDowall 1972; McDowall et al. 2001). There is no compelling reason to consider that diadromy has evolved in any of these galaxiids in New Zealand, but rather it probably reflects a common ancestry shared with diadromous Australian galaxiids, and diadromy could have evolved in any of the lands where these species are now found (or, in theory, even elsewhere).

In terms of their phylogenetic relationships, the galaxiids have been shown to have quite close affinities with another local group of fish genera, *Prototroctes*, *Retropinna* and *Stokellia*, the southern graylings and smelts (discussed in the previous section). These latter genera are found only in Australia and New Zealand (including the Chathams), and given the relationships to the galaxiids (McDowall 1969; Fink 1984; Johnson and Patterson 1996; Waters et al. 2000, 2002) these all appear to have evolved at least in southern latitudes. The group as a whole may be regarded as Gondwanan in origin, though not necessarily Gondwanan in terms of the present geographical range – the Gondwanan appearance may be coincidental.

7.6 Family Pinguipedidae

The single species of torrentfish, *Cheimarrichthys* (Fig. 7.5), in my view, has affinities with the blue cod, *Parapercis colias*, from New Zealand's coastal seas in the family Pinguipedidae (McDowall 1973b), though some ichthyologists place this fish in its own, monospecific family (Pietsch 1989; Nelson 2006). Which ever view is adopted, the torrentfish seems likely to share a common ancestry among marine trachinoid fishes, perhaps around the shores of New Zealand, as there are no potentially-related trachinoid freshwater species anywhere. As it is also the only diadromous (or freshwater-living) species among the entire trachinoid fishes (McDowall 1973a; Pietsch 1989), amphidromy is an independent local adaptation. Looking more widely at where *Parapercis* is found, it turns out to have quite wide Indo-Pacific relationships. So *Cheimarrichthys* can logically be seen as part of an Indo-Pacific group perhaps with its nearest relationships in New Zealand seas.

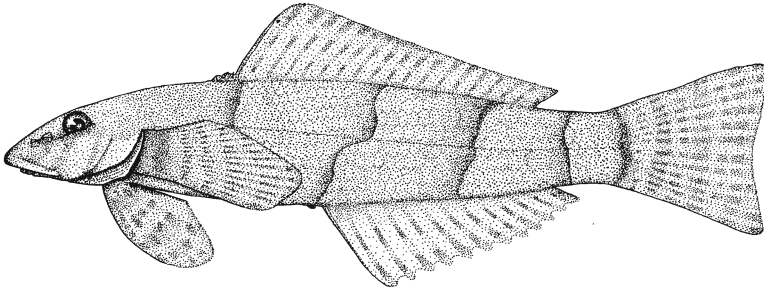


Fig. 7.5 Torrentfish, *Cheimarrichthys fosteri*, 105 mm TL (family Pinguipedidae): a local invader from New Zealand coastal seas

7.7 Family Eleotridae

There are seven described New Zealand species in the genus *Gobiomorphus* (see Figs. 1.6 and 1.7) (and perhaps some unrecognised taxonomic diversity) that are congeneric with two further species in eastern Australia. *Gobiomorphus* belongs in the family Eleotridae, which is a very widespread family found in lands bordering the tropics and subtropics of all the major oceans – Pacific, Indian and Atlantic (Thacker 2003; Thacker and Hardman 2005; Stevens and Hicks 2009). New Zealand's seven species of *Gobiomorphus* (McDowall 1975, 1990), four of them diadromous, are presently regarded as congeneric with an additional two species in eastern Australia (Larson and Hoese 1996) that may also be diadromous (McDowall 1988; Miles et al. 2009). Stevens and Hicks (2009) provide mtDNA sequence data, which show that the New Zealand species form a monophyletic sister clade to the Australian species, with New Zealand's amphidromous bluegill bully being the basal species. It therefore seems that diadromy either arrived or evolved, in New Zealand just once.

7.8 Family Pleuronectidae

The black flounder, *Rhombosolea retiaria*, is the only diadromous/freshwater flounder in the Australian/New Zealand genus *Rhombosolea* (f. Pleuronectidae – the 'right-eye flounders: Nelson 2006); it is catadromous. The black flounder seems unarguably to be a locally-evolved derivative of, or at least shares a common ancestry with, an as-yet unidentified *Rhombosolea* flounder living in New Zealand seas (though the genus is found also in southern Australia and Tasmania). Its diadromy is unarguably locally-evolved as it is the only species that is diadromous, and the species remains locked into reproduction at sea, as is true of its entirely marine congeners. The adults migrate to sea to spawn, possibly in spring (Taylor 1944), though little is known (McDowall 1990).

7.9 The Question of Southern Relationships

The distinctly southern pouched lamprey and the galaxiid/retropinnid lineages are all regarded as being southern cool-temperate homologues of the northern cool temperate lampreys, and the osmerid fishes or northern smelts (McDowall 1969; Johnson and Patterson 1996), and so we see here two groups living in similar high latitudes of the Northern and Southern Hemispheres, and they can together be described as ‘sister taxa’ with relationships that are ‘bi-polar’ or ‘bi-zonal’ or ‘bi-’ or ‘amphi-temperate’ – a variety of terms have been used for this phenomenon (Hubbs 1952; Darlington 1957, 1965; Briggs 1987). Thus, with c. 25 species involved in these groups in New Zealand, alone, we can see that New Zealand has a major component of the group that is southern in range and is related to a comparable northern group.

7.10 General Relationships of the Fauna

If we now seek to group the whole fauna according to its generalised distributions and relationships, the following assemblages are evident. All of the families represented in the New Zealand freshwater fish fauna usually have confamilial species elsewhere in the southwestern Pacific and/or southern cool temperate latitudes of the earth. It is notable that all of these groups maintain strong connections with the seas around New Zealand, to the extent that all of them in some families and many of them in the others, are diadromous and spend a significant part of their lives in the sea (see Chapter 5: Some essentials of freshwater fish biogeography).

Clearly there is a strong, distinctly southern, cool-temperate element in the fauna, which certainly includes the lamprey and the galaxiids. We can, I think, add the retropinnids to the ‘southern’ element since although they are essentially ‘Australasian’, their affinities lie with the other cool-temperate southern families, and, as noted earlier, all of these can be seen to be the southern counterparts of a northern cool-temperate groups. The similarities in the Australasian distributions patterns between the retropinnids and eleotrids are in my opinion misleading: they do not in my view indicate a shared or common ancestry or range.

Gobiomorphus (Fig. 7.6), instead of being part of a southern group, is really part of a much warmer water assemblage that happens to find the southernmost extremity of its range in New Zealand (reaching as far south as 47°S latitude, on Stewart Island); it really belongs more with fishes from the subtropics where the family Eleotridae is widespread in all oceans and is often diadromous (McDowall 1988; Thacker 2003; Thacker and Hardman 2005). The New Zealand species of *Gobiomorphus* on Stewart Island, in far southern New Zealand, and also in the submontane elevations of inland Central Otago, seem clearly to occupy the coldest habitats known for the whole family Eleotridae and, in fact *Gobiomorphus* seems to be struggling to maintain a presence in some of these waterways where it is quite

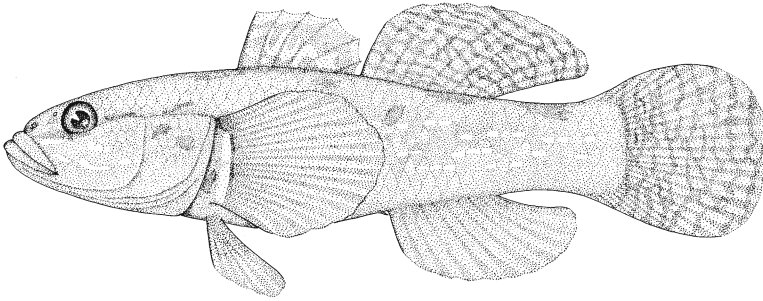


Fig. 7.6 Giant bully, *Gobiomorphus gobioides*, 174 mm TL (family Eleotridae): representative of the second largest radiation of freshwater fishes in New Zealand (genus shared with southeastern Australia)

rare – though the fossil evidence shows that the family has been in New Zealand since at least the Miocene (McDowall et al. 2006). That being so, eleotrids seem to have survived the Pleistocene glaciations somewhere in New Zealand, unless the extant stocks represent a secondary invasion from Australia.

As noted above, the torrentfish and black flounder both have their closest relationships in the seas around New Zealand, but if we seek some more explicit, broader, understanding of their relationships these appear also to belong to groups in Australia and more widely across the Indo-Pacific, rather than to others in southern cool-temperate lands. In both torrentfish and black flounder we see two instances in which diadromy appears to have evolved locally, making it of particular interest to an interpretation of the adaptive advantages of diadromy (McDowall 2004a).

Diadromy seems to be varyingly mandatory across these groups. It is absolutely mandatory in the pouched lamprey, in which there are neither non-anadromous populations nor fluvial sister species (like those in several northern lampreys and also the Australian lamprey genus *Mordacia* – Hubbs and Potter 1986), as it is also in *Anguilla*. The New Zealand grayling is always diadromous (as is its Australian congener), and although the New Zealand common smelt has many landlocked populations, Stokell's smelt is always diadromous. Among the diadromous galaxiids, only the shortjaw kokopu, *Gl. postvectis*, is an obligate diadromous species. However, among the four diadromous *Gobiomorphus* species only one is facultatively diadromous, this being the common bully, *Gb. cotidianus*. Interestingly, neither the torrentfish nor the black flounder has been able to establish lacustrine, non-diadromous populations (as has often happened in many other diadromous fishes, including in New Zealand – McDowall 1988, 1990, and as mentioned above), though the torrentfish has successfully shifted its reproductive biome from the sea (where all other pinguipedids reproduce) into fresh water, and that is, in itself, of interest. The common suggestion, that the reproductive biome of a species is indicative of its ancestral biome, is clearly sometimes untrue in this instance, as well as in various other diadromous groups, such as the anadromous gadid, *Microgadus tomcod*, in boreal North America, and there are other examples (McDowall 1988).

Summarising: diadromy seems clearly to have evolved twice in New Zealand, and in both instances from a marine ancestry (torrentfish and black flounder). It may otherwise have either arrived or evolved in, New Zealand at least ten additional times, as the New Zealand fauna has much shared ancestry with the freshwater fish fauna of southeastern Australia. Additional examples may be revealed by phylogenetic studies. Thus, it is unclear, in at least some instances, whether diadromy is an adaptive behaviour that was inherited from an ancestral form, or a physiological imperative (or maybe sometimes both of these). The number of times it has been lost from various clades is important.

And, viewed broadly, both life history data and molecular data suggest that:

- (i) Much of the New Zealand freshwater fish fauna shares a common ancestry with the Australian/Tasmanian fauna (McDowall 2002a).
- (ii) Where known the ages of lineage splits are probably much too recent for them to have been present on an unfragmented Gondwana.
- (iii) The New Zealand fauna probably has its origins in transoceanic dispersal from Australia c. 2,000 km across the Tasman Sea to the west (Waters and Burridge 1999; Waters et al. 2000; McDowall 1964, 2002a).

Given these patterns of distribution and affinity, perhaps Australia and New Zealand should be seen as a nexus of two widespread freshwater fish faunas – one southern cool-temperate and giving the appearance of a classically Gondwanan group, the other Indo-Pacific and unrelated to any Gondwanan lineages. Cooper and Millener (1993) observed that of the New Zealand biota generally, the “prevailing westerly winds and ocean currents have ensured that Australia has been the dominant source of immigrant species, especially in the late Cenozoic”, and this generalisation seems entirely applicable to the origins of the freshwater fish fauna (McDowall 1964, 2002a), with transport in oceanic currents the likely mechanism, but that is not essential, and New Zealand could have been a source, as has been suggested for some botanical groups. These issues are discussed in detail in Chapter 8.

7.11 Ancestry of Non-diadromous Species

Many of New Zealand's non-diadromous fish species, where relationships are known, appear to share a common ancestry with diadromous species:

- Molecular studies are suggesting that the *Gl. vulgaris* species complex is likely to be derived from the diadromous koaro (McDowall 1970); this could have been either a single or multiple derivation: the genetic evidence is not entirely consistent on this point (King and Wallis 1998; Waters and Wallis 2000, 2001a, b; Waters et al. 2001; Wallis et al. 2001) (Fig. 7.7).
- The ancestry and relationships of the ‘pencil galaxias’ species complex (*Gl. divergens*, *Gl. paucispondylus*, *Gl. macronasus*, *Gl. prognathus* and *Gl. cobitinis*) are at present uncertain, but the group could have ancient, independent, roots within the Galaxiidae that are not necessarily in New Zealand – a question that needs study.

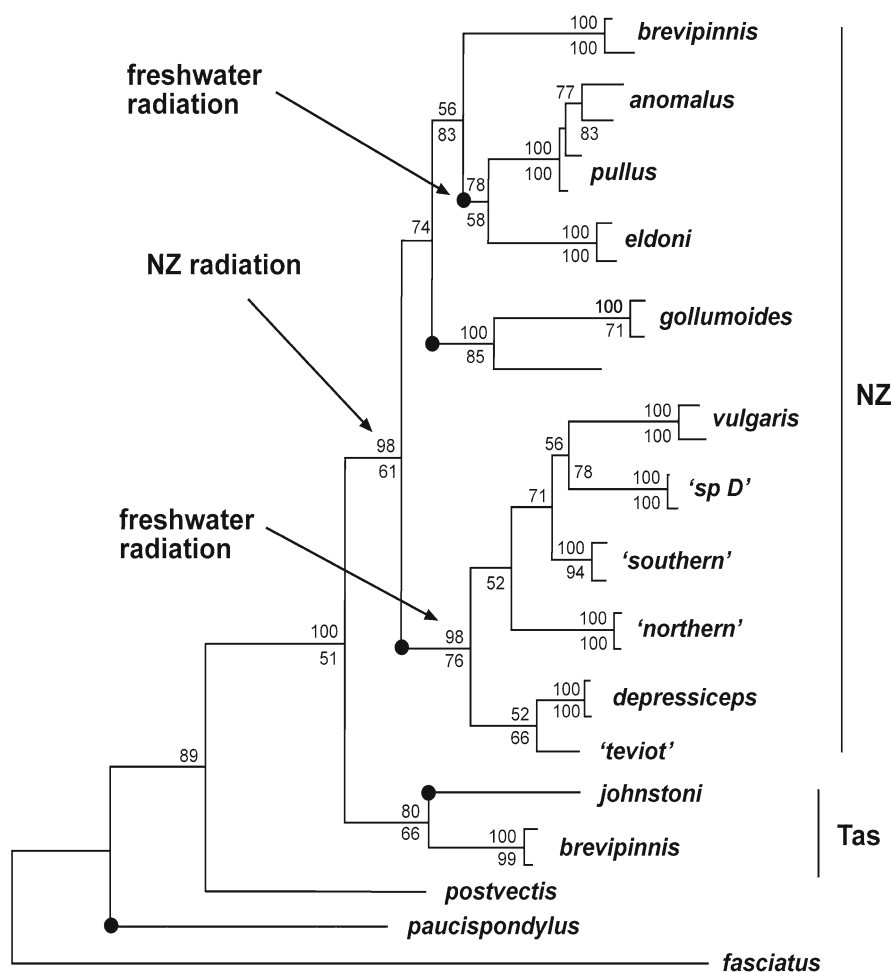


Fig. 7.7 One interpretation of the phylogenetic relationships of the *Galaxias vulgaris* species complex in southern New Zealand, based on mtDNA sequences and indicating dual derivations of non-migratory lineages from the widespread, diadromous *G. brevipinnis* (adapted from Waters and Wallis, 2001a) (n.b. additional DNA sequences using nuclear DNA are not entirely consistent with this arrangement, and may be suggesting a single derivation)

- The New Zealand's *Neochanna* mudfishes, though sharing a common ancestry with the diadromous Tasmanian mudfish (Fig. 7.4), have become wholly fresh-water-living in New Zealand – though they probably have not always been (McDowall 2004b; Waters and McDowall 2005). The genus almost certainly reached New Zealand through the sea, involving the amphidromous Tasmanian mudfish, *N. cleaveri* (Fulton 1986). Flannery (1984) predicted that if it “proves to be the case that these [New Zealand] mudfish are most closely related to the Tasmanian freshwater mudfish ... even dispersalists such as McDowall will

concede their probable Gondwanan origin (McDowall 1984)", but this is not so! Morphological and molecular data do both support such a shared common ancestry of the Tasmanian and New Zealand mudfishes (McDowall 1997, 2004b; Waters and White 1997; Waters and McDowall 2005). But what neither Flannery, nor I, were formerly aware of was that the Tasmanian mudfish species has a diadromous whitebait juvenile (as shown by Fulton 1986). Moreover, molecular data suggest a lineage split between the Tasmanian and New Zealand species that is only around 10 million years ago, and it is thus far too recent for Gondwana to be implicated (Waters and McDowall 2005). Patterns of distribution in relation to amphidromy in *Neochanna*, may not be simple for *N. rekohua*, if marine dispersal was needed to get *Neochanna* to the Chatham Islands, if it is accepted that the islands only emerged from the sea in the past few million years (Campbell and Hutching 2007).

- The lacustrine dune lakes galaxias is thought to be a lake derivative of inanga (McDowall 1970) and the populations presently included in this species (McDowall 1972, 1990) may have more than one genealogical origin in diadromous inanga stocks (Ling et al. 2001); study is needed.
- The Tarnedale bully is regarded as a lacustrine derivative of common bully (McDowall 1994); I reject the conclusion of Smith et al. (2003) that it is no more than an ecophenotype of that species (McDowall and Stevens 2007, and see Stevens and Hicks 2009; see also Chapter 15).

Much of the remainder of this book will explore some deep dichotomies in the biogeography of the fauna as a whole across the New Zealand landscape that are related very clearly and explicitly to whether species are diadromous or not.

References

- Aoyama J (2003) Origin and evolution of the freshwater eels, genus *Anguilla*. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel biology. Springer, New York, pp 19–29
- Baker AJ, Huynen LJ, Haddrath O, Miller CD, Lambert DM (2005) Reconstructing the tempo and mode of evolution in an extinct clade of birds with DNA: the giant moas of New Zealand. *Proc Nat Acad Sci USA* 102:8257–8262
- Bertin L (1956) Eels: a biological study. Cleaver and Hume, London, 192 pp
- Briggs JC (1987) Antitropical distribution and evolution in the Indo-West Pacific Ocean. *Syst Zool* 36:237–247
- Brooks DR (1985) Historical ecology: a new approach to studying the evolution of ecological associations. *Ann Missouri Bot Gard* 72:660–680
- Brooks DR, McLennan DA (2001) A comparison of a discovery-based and an event-based method of historical biogeography. *J Biogeogr* 28:757–767
- Brooks DR, McLennan DA (2002) The nature of diversity: an evolutionary voyage of discovery. University of Chicago, Chicago, IL, 668 pp
- Brundin L (1965) On the real nature of trans-Antarctic relationships. *Evolution* 19:496–505
- Brundin L (1966) Trans-Antarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagyiidae. *Kung Sven Vetenskap Hand* 11:1–472
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, 238 pp

- Cook LG, Crisp MD (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwana radiation. *Proc R Soc Lond B Biol Sci* 272:2535–2544
- Cooper A, Mourer-Chauvire C, Chambers GK, von Haeseler A, Wills AC, Paabo S (1992) Independent origin of New Zealand moas and kiwis. *Proc Nat Acad Sci USA* 89:8471–8744
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Crook DA, McDonald JI, Raadik T (2008) Evidence of diadromous movements in a coastal population of southern smelts (Retropinninae: *Retropinna*) from Victoria, Australia. *Mar Freshwater Res* 59:638–646
- Darlington PJ (1957) Zoogeography: the geographical distribution of animals. Wiley, New York, 675 pp
- Darlington PJ (1965) Biogeography of the southern end of the world. Harvard University Press, Cambridge, MA, 236 pp
- Day F (1888) Supplement to the fishes of India, being a natural history of the fishes known to inhabit the seas and freshwaters of India, Burma and Ceylon. Williams & Norgate, London, pp 779–816
- Eikaas H, McIntosh AR (2006) Habitat loss through disruption of constrained dispersal networks. *Ecol Appl* 16:987–998
- Eikaas H, Harding JS, Kliskey AD, McIntosh AR (2005) The effect of terrestrial habitat fragmentation on fish populations in small streams: a case study from New Zealand. *Norweg J Geog* 59:269–275
- Eikaas H, Kliskey AD, McIntosh AR (2006) Analysis of patterns in diadromous fish distributions using GIS. *Trans GIS* 10:469–483
- Fink WL (1984) Basal euteleosts: relationships. *Am Soc Ichthyol Herpetol Spec Publ* 1:201–206
- Flannery T (1984) New Zealand: a curious zoogeographic history. In: Archer M, Clayton G (eds) Vertebrate zoogeography and evolution in Australasia (animals in space and time). Hesperian Press, Carlisle, NSW, pp 1089–1094
- Fulton W (1986) The Tasmanian mudfish, *Galaxias cleaveri*. *Fish Sahul* 4:150–151
- Gill HS, Renaud CB, Chapleau F, Mayden RL, Potter IC (2003) Phylogeny of living parasitic lampreys (Petromyzontiformes) based on morphological data. *Copeia* 2003:687–703
- Gibbs GW (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton, Nelson, N Z, 232 pp
- Gorham S (1977) Notes on a collection of fishes from the Falkland Islands. *Falkland Isl J* 1977:43–52
- Haddrath A, Baker AJ (2001) Complete mitochondrial DNA sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proc R Soc Lond B Biol Sci* 268:939–945
- Harvey PH (1996) Phylogenies for ecologists. *J Anim Ecol* 65:255–263
- Hayes JW, Leathwick JR, Hanchet SM (1989) Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *N Z J Mar Freshwater Res* 23:171–180
- Hector J (1872) Notes on the edible fishes. In: Hector J, Hutton FW (eds) Fishes of New Zealand. Hughes, Wellington, pp 97–133
- Hubbs CL (1952) Antitropical distributions of fishes and other organisms. *Proc 7th Pac Sci Congr* 3:324–329
- Hubbs CL, Potter IC (1986) Distribution, phylogeny and taxonomy. In: Hardisty MW, Potter IC (eds) The biology of lampreys, 1. Academic, London, pp 1–6
- Jellyman DJ, Chisnall BL, Dijkstra LH, Boubée JAT (1996) First record of the Australian long-finned eel, *Anguilla reinhardtii*, in New Zealand. *Mar Freshwater Res* 47:1037–1040
- Jellyman DJ, Bowen MM (2009) Modeling larval migration routes and spawning areas of anguillid eels of New Zealand. *Amer Fish Soc Symp* 69:255–274
- Johnson GD, Patterson C (1996) Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic, San Diego, CA, pp 252–332

- Joy MK, Death RG (2000) Development and application of a predictive model of riverine fish community assemblages in the Taranaki region of the North Island, New Zealand. *N Z J Mar Freshwater Res* 34:241–252
- Joy MK, Death RG (2002) Predictive modelling of freshwater fish as a biomonitoring tool in New Zealand. *Freshwater Biol* 47:2261–2275
- King TM, Wallis GP (1998) Fine-scale genetic structuring in endemic galaxiid fish populations of the Taieri River. *N Z J Zool* 25:17–22
- Knapp M, Stockler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ (2005) Relaxed molecular clock provides evidence for long-distance dispersal by *Nothofagus* (southern beech). *PLoS Biol* 3:38–43
- Knapp M, Mudalier R, Havell D, Wagstaff SJ, Lockhart PJ (2007) The drowning of New Zealand and the problem of *Agathis*. *Syst Biol* 56:862–870
- Larson HK, Hoese DF (1996) Gudgeons. In: McDowall RM (ed) *Freshwater fishes of South-eastern Australia*. Reed, Chatswood, NSW, pp 200–219
- Leathwick JR, Rowe DK, Richardson J, Elith J, Hastie T (2005) Using multivariate regression splines to predict the distributions of New Zealand diadromous fish. *Freshwater Biol* 50:2034–2052
- Leathwick JR, Elith J, Chadderton WL, Rowe DK, Hastie T (2008) Dispersal, disturbance and the contrasting biogeographies of New Zealand diadromous and non-diadromous freshwater fish species. *J Biogeogr* 35:1481–1497
- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species; the ‘new’ biodiversity and evolutionary significant units among New Zealand’s galaxiid fishes. *J Fish Biol* 59(Suppl A):209–222
- McCleave JD, Edeline E (2009) Diadromy as a conditional strategy: patterns and drivers of eel movements in continental habitats. *Amer Fish Soc Symp* 69:97–120
- McDowall RM (1964) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool, Harv Univ* 139:341–431
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *J R Soc N Z* 2:325–367
- McDowall RM (1973a) *Galaxias indicus* Day, 1888: a nomen dubium. *J R Soc N Z* 3:191–192
- McDowall RM (1973b) The relationships and taxonomy of the New Zealand torrent fish, *Cheimarrichthys fosteri* Haast (Pisces: Mugiloididae). *J R Soc N Z* 3:199–217
- McDowall RM (1975) A revision of the New Zealand species of *Gobiomorphus* (Pisces: Eleotridae). *Nat Mus N Z Rec* 1:1–32
- McDowall RM (1979) Fishes of the family Retropinnidae (Pisces: Salmoniformes): a taxonomic revision and synopsis. *J R Soc N Z* 9:85–121
- McDowall RM (1984) *The New Zealand whitebait book*. Reed, Wellington, N Z, 210 pp
- McDowall RM (1988) *Diadromy in fishes: migrations between freshwater and marine environments*. Croom Helm, London, 309 pp
- McDowall RM (1990) *New Zealand freshwater fishes: a natural history and guide*. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1993) Implications of diadromy for the structuring and modelling of riverine fish communities in New Zealand. *N Z J Mar Freshwater Res* 27:453–462
- McDowall RM (1994) The Tarndale bully, *Gobiomorphus alpinus* (Pisces: Eleotridae) revisited and redescribed. *J R Soc N Z* 24:117–124
- McDowall RM (1996a) Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Can J Fish Aquat Sci* 53(Suppl 1):219–236
- McDowall RM (1996b) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148

- McDowall RM (1996c) Family Prototroctidae – southern graylings. In: McDowall RM (ed) Freshwater fishes of southeastern Australia. Reed, Chatswood, NSW, pp 96–98
- McDowall RM (1997) Affinities, generic classification, and biogeography of the Australian and New Zealand mudfishes (Salmoniformes: Galaxiidae). Rec Aust Mus 49:121–137
- McDowall RM (1998) Driven by diadromy: its role in the historical and ecological biogeography of New Zealand freshwater fishes. Ital J Zool 65(Suppl S):73–85
- McDowall RM (2002a) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. J Biogeogr 29:207–220
- McDowall RM (2002b) Like a thief in the night. Fish Game N Z 37:34–36
- McDowall RM (2004a) Ancestry and amphidromy in island freshwater fish faunas. Fish Fisher 5:75–85
- McDowall RM (2004b) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). J R Soc N Z 34:315–331
- McDowall RM, Fulton W (1996) Family Galaxiidae: galaxiids. In: McDowall RM (ed) Freshwater fishes of southeastern Australia. Reed, Chatswood, NSW, pp 52–77
- McDowall RM, Stevens MA (2007) Taxonomic status of the Tairāwhiti bully *Gobiomorphus alpinus* (Teleostei: Eleotridae), revisited – again. J R Soc N Z 37:15–29
- McDowall RM, Taylor MJ (2000) Environmental indicators of habitat quality in a migratory freshwater fish fauna. Environ Manag 25:357–374
- McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands freshwater fishes. Aquatic Conserv Mar Freshwater Ecosyst 11:473–486
- McDowall RM, Allibone RM, Chadderton WL (2005) Falkland Islands freshwater fishes: a natural history. Falklands Conservation, London, 102 pp
- McDowall RM, Jellyman DJ, Dijkstra LH (1998) Arrival of an Australian anguillid eel in New Zealand: an example of transoceanic dispersal. Environ Biol Fish 51:1–6
- McDowall RM, Kennedy EM, Lindqvist JK, Lee DE, Alloway BV, Gregory MR (2006) Probable *Gobiomorphus* fossils from the Miocene and Pleistocene of New Zealand (Teleostei: Eleotridae). J R Soc N Z 36:97–109
- McGlone MS (2005) Goodbye Gondwana. J Biogeogr 32:739–749
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of biota. Ecol Stud 186:17–32
- Miles NG, West RJ, Norman ND (2009) Does otolith chemistry indicate diadromous life cycles for five Australian riverine fishes. Mar Freshwat Res 60:904–911
- Nelson JS (2006) Fishes of the world, 4th edn. Wiley, New York, 601 pp
- Phillipps WJ (1925) New Zealand eels. N Z J Sci Tech 8:28–30
- Pietsch TW (1989) Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989:253–303
- Potter IC (1996) Family Mordaciidae: shortheaded lampreys. In: McDowall RM (ed) Freshwater fishes of southeastern Australia. Reed, Chatswood, NSW, pp 32–35
- Potter IC, Prince PA, Croxall JP (1979) Data on the adult marine and migratory phases in the life cycle of the Southern Hemisphere lamprey *Geotria australis* Gray. Environ Biol Fish 4:65–69
- Ross K (2009) Freshwater fish in the Falklands: conservation of native zebra trout. A report to the Falkland Islands Government and Falklands Conservation, 36 pp
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tairāwhiti bully revisited with molecular markers: an ecophenotype of the common bully *Gobiomorphus cotidianus* (Pisces: Gobiidae). J R Soc N Z 33:663–673
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. Evol Ecol Res 11:109–123
- Stockler K, Daniel IL, Lockhart PJ (2002) New Zealand kauri (*Agathis australis* (D. Don.) Lind., Araucariaceae) survives Oligocene drowning. Syst Biol 51:827–832

- Swenson U, Backlund A, McLoughlin S, Hill RS (2001) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* 17:28–47
- Taylor WA (1944) Waihora: Maori associations with Lake Ellesmere. *Ellesmere Guardian*, Leeston, N Z, 26 pp
- Tesch FW (2003) *The eel*. Blackwell, Oxford, 408 pp
- Thacker CE (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Mol Phyl Evol* 26:354–368
- Thacker CE, Hardman MA (2005) Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidei). *Mol Phyl Evol* 37:858–871
- Thillart G, van den, Dufour S, Rankin JF (2009) Spawning migration of the European eel: reproduction index, a useful tool for conservation management. Springer, New York
- Tsakamoto K, Aoyama J (1998) Evolution of freshwater eels of the genus *Anguilla*: a probable scenario. *Environ Biol Fish* 52:138–149
- Tsakamoto K, Nakae I (1998) Do all freshwater eels migrate? *Nature* 396:935
- Tsakamoto K, Aoyama J, Miller MJ (2002) Migration, speciation and the evolution of diadromy in anguillid eels. *Can J Fish Aquat Sci* 59:1989–1998
- Wallis GP, Treweek SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Wallis GP, Judge KF, Bland J, Waters JM, Berra TM (2001) Genetic diversity in New Zealand *Galaxias vulgaris* sensu lato (Teleostei: Osmeriformes: Galaxiidae): a test of a biogeographic hypothesis. *J Biogeogr* 28:59–67
- Waters JM, Burrridge CP (1999) Extreme intraspecific mitochondrial DNA sequence divergence in *Galaxias maculatus* (Osteichthyes: Galaxiidae), one of the world's most widespread freshwater fish. *Mol Phyl Evol* 11:1–12
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, Wallis GP (2000) Across the Southern Alps by river capture? Freshwater fish phylogeography in South Island, New Zealand. *Mol Ecol* 9:1577–1582
- Waters JM, Wallis GP (2001a) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Wallis GP (2001b) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *J Fish Biol* 58:1166–1180
- Waters JM, White RWG (1997) Molecular phylogeny and biogeography of the Tasmanian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Aust J Zool* 45:39–48
- Waters JM, Dijkstra LH, Wallis GP (2000) Biogeography of a Southern Hemisphere freshwater fish: how important is marine dispersal? *Mol Ecol* 9:1815–1821
- Waters JM, Esa YB, Wallis GP (2001) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298
- Waters JM, Saruwatari T, Kobayashi T, Oohara T, McDowall RM, Wallis GP (2002) Phylogenetic placement of retropinnid fishes: data set incongruence can be reduced by using asymmetric character state transformations. *Syst Biol* 51:432–449
- Wiens JJ, O'Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19:640–644
- Winkworth RC, Wagstaff SJ, Glenn D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ, Div Evol* 5:327–247

Chapter 8

Galaxias and Gondwana

Abstract Galaxiidae are present on nearly all former Gondwanan lands: Australia, New Caledonia, New Zealand, Patagonian South America, the Falkland Islands, southern Africa and various other small islands associated with these lands. However, it seems unlikely that this broad, apparently Gondwanan, range derives explicitly from vicariant processes relating to continental drift, plate tectonics and the fragmentation of Gondwana. Diadromy is widespread in the family, and widespread diadromous species, variously present on two or more of Australia, New Zealand, Patagonia and the Falklands, suggest that the faunas of these southern lands were strongly influenced by transoceanic dispersal, though contrary views are argued vigorously. Views relating to these dispersal origins date back the writings of Darwin in the late nineteenth century and were canvassed widely by other biogeographers, though some found the idea of dispersal unlikely, despite the widespread presence of diadromy in the fauna.

Keywords Charles Darwin • Continental drift • Diadromy • Dispersal • Galaxiidae • Gondwana • History • Life history • Plate tectonics

8.1 The Galaxiid Fishes

No account of the biogeography of New Zealand's freshwater fishes could be regarded as complete without a discussion of the details of the *Galaxias*/Gondwana connection, including a rather wider purview of the Galaxiidae than just the New Zealand species. From the earliest discovery of the galaxiid fishes there was debate and confusion about what these small fish were related to and about how an ostensibly freshwater fish group, like Galaxiidae, could have achieved its broad and exclusively southern cool-temperate distribution. Some early opinions connected them phylogenetically to the northern-temperate pikes, family Esocidae (Berg 1940; discussed in McDowall 1969, 1970a). Equally, there was much discussion amongst nineteenth and early twentieth century ichthyologists and biogeographers of the group's geographical distribution, and how this developed across earth history. It was a question causing deep perplexity,

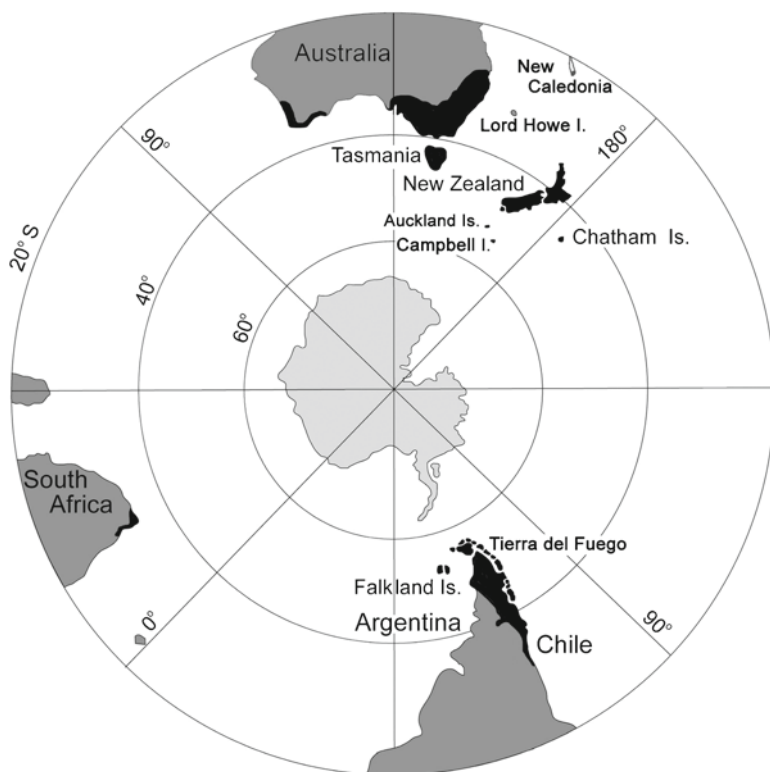


Fig. 8.1 Very broad distribution of fishes of the family Galaxiidae around the Southern Ocean, interpreted by some commentators as reflecting a Gondwanan ancestry, though data from the molecular clock do not support this interpretation

prompting many questions and intense debate. There was a sense in which the group's biogeography was seen as even more difficult than for other, perhaps better-known and more widely-discussed, iconic groups like the southern beech trees of the genus *Nothofagus*, or the ratite birds, for at least these groups could survive out of water, where the galaxiids couldn't.

Fishes of the family of Galaxiidae are found very widely at middle latitudes around the Southern Hemisphere (Fig. 8.1). To summarise, they are found:

- South of about latitude 30°S in Western Australia
- South of about 28°S in eastern Australia
- Widely on Tasmania
- Near the southern tip of New Caledonia at latitude ca. 22°S (and at an elevation of ca. 250 m, at about the highest elevation, coolest, freshwater habitat available to fish there)
- On Lord Howe Island at latitude 31.5°S
- Throughout New Zealand, and on the Chatham, Auckland and Campbell Islands, extending south as far as 52.5°S

- In Patagonian Chile south of about latitude 32°S
- Also in Patagonian Argentina to its southern limits on islands to the south of Tierra del Fuego (ca. 55°S)
- On the Falkland Islands at about latitude ca. 52°S
- And in southern Africa (south of ca. 32°S)

As pointed out in the previous chapter, an early record of a galaxiid from India (Day 1888) has never been confirmed and this is now rejected (McDowall 1973b); had there actually been a galaxiid in India, the family would have appeared even more ‘Gondwanan’ than it does.

Even without the Indian record, the family Galaxiidae certainly ranks as a distinctly characteristic “Gondwanan” group. Meek (1916: 145) long ago thought that “special interest attaches to these families from their peculiar distribution around the temperate waters of the Southern Hemisphere” and though he was far from the first to engage in this problem, he put it about as bluntly and crisply as we could hope to.

American biogeographer Philip Darlington (1965: 141) cited the tree genus *Nothofagus* as more characteristic of the southern cold temperate zone than any other group and, although this is not a ‘competition’, it seems to me that the mantle belongs equally appropriately to some other groups, including the ratite birds (kiwis, moas, ostrich, emu and other flightless birds) and, of particular present importance, the galaxiid fishes. These fishes are present almost everywhere that *Nothofagus* is (except in Papua-New Guinea) and, moreover, *Galaxias* is found substantially more widely on southern lands than *Nothofagus* is (which is absent from such galaxiid strongholds as Western Australia, Lord Howe Island, the Auckland, Campbell and Chatham Islands, the Falkland Islands, and southern Africa). Certainly, the fossil record of *Nothofagus* is much more complete, its distribution formerly included Antarctica, and this tree genus is known across geological time (as fossil pollen – Couper 1960; Hill 2001) in a way that *Galaxias* is not (though pollen evidence can be misleading owing to the huge distances that it can be carried by wind, leading to its being present in deposits on Tristan da Cunha and Gough Islands, > ca. 7,200 and 4,800 km away from the nearest *Nothofagus* forests in Patagonia). We need to recognise, however, that pollen preserves well and easily in the geological record in a way that small fishes do not. Regardless, galaxiids certainly have a very strong ‘Gondwanan’ appearance and the family’s distribution has generated a great deal of discussion over more than 150 years, being described most recently as an iconic Southern Hemisphere group by BurrIDGE et al. (2009). Ratites are also very widespread in southern lands, being represented on Africa, Madagascar, Papua-New Guinea, Australia, New Zealand and South America, and there are other groups such as the parastacid freshwater crayfishes, among quite a diversity of groups that are also characteristically Gondwanan.

Another distinctly ‘Gondwanan’ group, or so it seems from a brief inspection, is the primitive plant family Proteaceae, which Barker et al. (2007) report as present in southern Africa, Australia, Tasmania, New Zealand, South America, New Caledonia, New Guinea, Southeast Asia, and Sulawesi – 80 genera and 1,700 species “spread

over all Gondwana's current land masses except Antarctic and [according to Barker et al.]...this is an ideal group with which to test hypotheses of the biogeographical history of Gondwana's flora." In New Zealand the only proteacean is the monotypic tree genus *Knightia*, which Barker et al. (2007) regarded as "post-Gondwanan" there, and so a product of dispersal. Equally, New Caledonian proteaceans are also present there as an outcome of dispersal, if the conclusions of Grandcolas et al. (2008) are accepted, that New Caledonia was fully submerged by seas for millions of years in the early Cenozoic. So yet again, at least part of the range of a group of that is probably of Gondwanan age, and which may have achieved some or much of its range as a result of Gondwanan vicariance, seems also to have been influenced by post-Gondwanan dispersal – though how *much* dispersal is less easily quantified.

Darlington (1965: 67), summarising for South America, claimed that "there is simply no special, old, independent fauna of terrestrial vertebrates at the southern tip of South America, but just a modest accumulation of more or less cold-tolerant, not much differentiated, more or less recently derived representatives of groups that are widely distributed elsewhere on the continent.... In Australia-Tasmania, as in South America, there is simply no special, old, independent fauna of terrestrial vertebrates in the far south. It seems to me that this is the essential fact in southern biogeography." But, despite Darlington's strongly stated opinion, there *are* some distinctly southern vertebrate taxa in these lands, such as galaxiid fishes and ratite birds, and understanding their evolutionary and biogeographic histories is important to biogeography, more generally.

Recognition of the place of the former Mesozoic continents of Pangaea and Gondwana in biogeographic discussion has burgeoned in the past 30–40 years as plate tectonics became increasingly accepted by geologists, and it now provides a mechanism for explaining how continental drift takes place. As a result, biogeographers have increasingly recognised the significance of continental drift to the history of life on earth. This has substantially involved development of the fields of panbiogeography, and vicariance and cladistic biogeography (Croizat 1958, 1964; Nelson 1969; Rosen 1974a; Nelson and Ladiges 2001; Humphries and Parenti 1999; Wiley 1987, 1988; Briggs 2007, 2009). The implications of the former existence of Gondwana obviously have potentially been particularly significant for southern, or formerly southern lands, such as Australia, New Zealand, South America, Africa, India and Antarctica. However, these biogeographical developments have not been without controversy, substantially because of the tendency of some practitioners to seek universal biogeographical explanations in continental drift – what Simpson (1952) referred to as "'all-or-none' propositions in the form of Aristotelian 'either-or' dichotomies". Clearly, the history of life on earth has not been that simple, what ever might have been the role of Gondwana.

The distributions and biogeographies of a substantial number of major taxonomic groups have been repeatedly and particularly linked to the existence of Gondwana as a primary cause for biogeographic patterns. Among these groups, as noted above, have been such groups as the plant genus *Nothofagus* (Couper 1960; Darlington 1965), the ratite birds (Fleming 1979), the galaxiid fishes (Rosen 1974a; Campos

1984) and also the chironomid midges (Brundin 1965, 1966), small freshwater dipterans. Distributions of the members of each of these groups have repeatedly been attributed to their former presence on Gondwana, as commentators have decided, often *a priori*, that none of these groups is capable of naturally dispersing across the huge ocean gaps that now separate the southern lands on which they are found, lands that seem certain to have once been a part of Gondwana. Some biogeographers have even claimed to have identified congruence between patterns in the fragmentation of Gondwana and the phylogenetic relationships of the biotic groups that live on these fragments, this ostensibly reinforcing the likelihood of Gondwana's seminal role, but I think it is all rather less simple than that.

Looking, briefly, at the biogeography of *Nothofagus* and the ratite birds: the broad, ostensibly Gondwanan geographical ranges of both groups have been shown, in the past decade or so, to almost certainly have been generated substantially by transoceanic dispersal, and this applies explicitly to their presence in New Zealand (Cooper et al. 1992; Swenson et al. 2001; Haddrath and Baker 2001; Knapp et al. 2005; Baker et al. 2005; Cook and Crisp 2005). Harshmann et al. (2008) wrote of ratites seeming to be “a textbook example of vicariance biogeography”, and of the “convenient serendipity of continental drift as a mechanistic explanation for ratite distribution prov[ing] irresistible”, but using molecular data, they have supported the conclusions of others, like Cooper et al. (1992) and Haddrath and Baker (2001), that the ratites are polyphyletic, and that the present distribution of the group may have involved transoceanic flight, at least in part. Wallis and Trewick (2009: 3556) have recently summarised that “kiwi ancestors arrived here...possibly through a New Caledonian arc, and cite the evidence of Harshmann et al. (2008) that “kiwi ancestors could even have been flighted.” Thus, although *Nothofagus* and the ratites were probably once present on an ancestral Gondwanan land-mass, there is an increasing recognition among biogeographers that that is only part of the story. Again, Wallis and Trewick (2009: 3556) concluded that evidence from area cladograms for *Nothofagus* are “at odds with continental break-up,” i.e., the pattern of taxonomic divisions among *Nothofagus* species is different from the pattern of break-up of originally Gondwanan land masses that have *Nothofagus*. And, in the end, even if the two patterns are congruent, a causal relationship cannot automatically be assumed for all or part of the pattern in *Nothofagus*. As Kodandaramaiah (2009) argued, we need to recognise the possibility that the distribution patterns of various taxa may be closely congruent, but result from different causal mechanisms as different as vicariance and dispersal, we need to also have some understanding of dispersal ability. As for the chironomids, although Brundin's work has been treated with enthusiasm by some as a proof of the validity of his biogeographic method, no-one has returned to these animals and used DNA sequencing to corroborate Brundin's phylogenetic hypotheses, which were based entirely on morphology, and there is a really fertile field for study there, to apply molecular techniques to the same group of taxa. I do not deal with these further, here, but turn to an account of the implications of these developments in biogeographic theory and practice for the galaxiid fishes.

8.2 The Early History of Galaxiid Biogeography

From almost their earliest discovery, the broad southern distribution of the fishes in the genus *Galaxias* generated comment. Darwin collected galaxiids from the Falkland Islands, southern Patagonia on the Beagle Channel and in northern New Zealand on the voyage of the Beagle in 1835 (Darwin 1896) and though the fish from these three places were described as three distinct species by Jenyns (1842 – originally in the genus *Mesotes*) all of the specimens were in fact conspecific, belonging to what is now known as *Gl. maculatus* (Stokell 1966; McDowall 1970a, 1972), with the Jenyns names *Gl. attenuatus* and *Gl. alpinus*, now treated as synonyms. Darwin (1873) regarded such a very broad range of an ostensibly freshwater fish genus as at least surprising, though he would have been even more surprised had he known that the three species described by Jenyns from specimens he had collected as he travelled around the Southern Hemisphere, actually represent a single widespread species. That issue aside, Darwin was just the first of many naturalists who have explored this issue and his comments were just the beginning of discussion that persisted for well over a century. British Museum ichthyologist, Albert Günther (1866) listed the galaxiid specimens in the collections of the British Museum from the Falklands, Tasmania, New Zealand, and some ostensibly from Peru, in the single species *Gl. attenuatus* (one of Jenyns's names). He did not formally assign Jenyns' *Gl. maculatus* to synonymy, though he did record *Gl. attenuatus* from 'southern parts of South America', roughly where Darwin had originally collected some.

Interestingly, although Günther (1866) recorded the family Galaxiidae as from "the temperate zone of the Southern Hemisphere," at that time he made no explicit comment on this huge and highly disjunct geographical range. However, in 1867, when describing another galaxiid (*Neochanna apoda* from New Zealand), Günther commented on the Galaxiidae, that: "Their geographical distribution is a point to which the greatest interest attaches.... The occurrence of the same natural genus of freshwater fishes in Australia, New Zealand, and South America would appear to be significant enough, and must be more so when we find that one and the same species (*Galaxias attenuatus*) inhabits the fresh waters of countries separated at present by the South Pacific Ocean. Nor does this fact stand alone, inasmuch as another family of freshwater fishes, that of the *Haplochitonidae* [sic], offers a very similar instance of geographical distribution – one of the two genera of which it is composed being found in Terra [sic] del Fuego and the Falkland Islands (*Haplochiton*) [sic], the other in Southern Australia (*Prototroctes*)."

In New Zealand, James Hector (1872) cited Günther, and presumably did so because he agreed with him, that *Galaxias* is related "perhaps to the African Mormyridae and the Arctic Esocidae", though he was well aware of the galaxiid migrations to and from the sea, as juveniles, and that these fish are implicated in a significant fishery that exploits these fish as they enter river estuaries from coastal seas, at least in New Zealand. There is a mix of mystery implicit here. As it happens, *Aplochiton* (as correctly spelt) and *Prototroctes* are not confamilial (McDowall

1969), though another later-recognised Australian genus, *Lovettia* (first described as *Haplochiton sealii* by the Tasmanian A.M. Johnston 1883) is accepted as confamilial with *Aplochiton*, while Günther (1870) would soon describe another species of *Prototroctes* from New Zealand, making that genus also common to both Australia and New Zealand. Clearly, the complex and astonishingly broad range of some of these southern freshwater fishes was beginning to be identified, though *Retropinna* and *Prototroctes* were then seen as related to the northern cold-temperate smelts of the family Osmeridae. As noted above, although the galaxiids were once connected to the pan-temperate northern pikes of the family Esocidae, eventually, all of the southern taxa would be shown to be quite closely related to each other, and all of these southern taxa to the Northern Hemisphere Osmeridae (McDowall 1969; Fink 1984; Johnson and Patterson 1996; Waters et al. 2000b; Ishiguro et al. 2003).

Darwin, himself, had begun to identify some of the biogeographical basis for these patterns. He had actually collected some of these fish from at least brackish water at the Falkland Islands, when travelling with the *Beagle* in the 1830s, and he commented in the 6th edition of “The Origin...” (Darwin 1873) that perhaps these fishes could endure marine salinities. He comments (p. 343–4) that “Dr. Günther has lately shown that the *Galaxias attenuatus* [= *Gl. maculatus*] inhabits Tasmania, New Zealand, the Falkland Islands, and the mainland of South America. This is a wonderful case, and probably indicates dispersal from an Antarctic centre during a former warm period.” However, Darwin also discussed, and at some length, the issues relating to the dispersal of freshwater fish, and he concluded “This case [i.e. Galaxiidae], however, is rendered in some degree less surprising by the species of this genus having the power of crossing by some unknown means considerable spaces of open ocean...” Just what he had in mind is a little obscure.

This does not, of course, mean that it was a simple matter for the family (and, indeed, for one species in the family) to become as widespread as it is, but during the late 1800s and early 1900s there would be a growing realisation, by the likes of Darwin, Günther, Boulenger, Regan, Meek, and others, that transoceanic dispersal might just be possible for galaxiids.

New Zealand naturalist Hutton (1873: 242), though he was well aware that some galaxiids migrate to and from the sea, argued that the galaxiid fishes “naturally supply more important evidence as to the former distribution of land than those [fishes] inhabiting the sea.” Nevertheless, he found the fact that New Zealand’s freshwater fishes exhibited only as much endemism as the marine fishes a “remarkable and unexpected result”. He concluded that for the marine fishes, this depended in part on the “permanency of specific characters since New Zealand was isolated [from other lands] and partly on the power possessed by fishes migrating to us from other countries, while among the fresh-water fish [he thought] the proportion depends entirely on permanency of specific characters”. Clearly, Hutton could countenance no dispersal through the sea by New Zealand’s freshwater fishes, even though he would have been well aware that some of them, at least, spent part of their lives at sea (Hutton 1872). And, despite this, he concluded (Hutton 1873: 243) that the “evidence, therefore, to be derived from the fresh-water fish goes to prove that a close connection has existed between Australia, New Zealand and South America”.

Pioneering evolutionist and biogeographer Alfred Wallace (1876), too, recognised the very broad range of the galaxiids and this led him to canvass the prospect that they may have been transported around the Southern Ocean trapped in Antarctic ice.

Hutton (1884: 15) later saw “*Galaxias*, *Cheimarrichthys* (an endemic genus allied to *Aphrites*), *Prototroctes*, and the Lampreys...” as “Antarctic” in distribution, and the anguillid, freshwater eels as “Australian or Polynesian”, but he regarded *Eleotris* (in which genus the New Zealand species of *Gobiomorphus* were originally placed – see McDowall 1975) as “an Indian archipelago and Australian genus...[that] also is found in Mexico and the West Indies...[that]...may also indicate a South American element”. I think this was the first real effort to place the New Zealand freshwater fish fauna in a broader global context, and given the knowledge of the time, his ideas can be viewed as distinctly insightful.

American ichthyologist Theodore Gill (1893) believed that “there may not have been a continuity of land at any one time between South America, Australia, and New Zealand, but at some remote period in the past it is at least possible that there was a region in which the Galaxiids and Haplochitonids [sic] were developed and, subsequently, representatives of these families might have found their way into the regions where they now abound. But it may be urged that such a derivation is only possible and there may have been other means for the diffusion of the same types.”

Gill concluded that, “in the present stage of science, then, we may be permitted to postulate that (fishes being congeneric in New Zealand, Australia and South America), that there existed some terrestrial passageway between the several regions as late as the close of the Mesozoic period”.

Gill’s opinion that land connections are necessary for the dispersal of galaxiids, a little later became rather firmer with a quote (Gill 1896) from Beddard (1895). He takes Beddard’s remarks on terrestrial annelids and applies them to galaxiids – “It is clear that if the former extension of the Antarctic continent is not believed some explanation of these remarkable facts is wanted; on that hypothesis they are perfectly explicable.”

Nineteenth century New Zealand colonial surveyor/naturalist Francis Clarke (1899) soon afterwards recognised that just as New Zealand “is famed for our remains of various struthious birds [kiwis and moas], so we should also gather ichthyological fame for the great number and varieties of these fishes [galaxiids], and it would be interesting if evidence should be obtained of their geological existence also.” He was insightful in recognising possible affinities between these New Zealand fishes and the Northern Hemisphere salmonids and their comparable distributions at high latitudes in both hemispheres. However, Clarke recognised that because *Gl. maculatus* is “ocean frequenting, its greater extension of habitat is not so much to be wondered at.” Clarke (1899) reported, too, that the young of *Gl. brevipinnis* (which he named as *Gl. robinsonii*) migrate from the sea. The Australian, Macleay (1883), was also clearly puzzled, concluding that “...there is no other way of accounting for the appearance of these fishes in such widely different localities” in New Zealand fresh waters. Hutton (1901) later described *Gl. bollansi*, as a distinct species, which was based on a galaxiid taken from the mouth of a cormorant on the remote Auckland Islands (which he presumed to actually have a marine origin, although wrongly, as it transpired).

British Museum ichthyologist George Boulenger (1900) reported observations by Rupert Vallentin at the Falkland Islands, that fish known to the inhabitants there as “smelt” were fairly common and occurred in shoals in the shallow water along the shore. The specimens brought home [by Vallentin] were dipped from the sea with a large hand net while being pursued by a penguin.” Clearly, it has long and widely been believed that the juveniles of *Gl. maculatus* migrate from the sea, and it was also (though wrongly) thought, by some observers, that they actually spawned there. Thus, although there was substantial confusion and bewilderment about the habits of the galaxiid fishes, by the late 1800s and early 1900s, reports were increasingly being published about their marine occurrence in some form or another.

It was in this climate of belief and understanding that Boulenger (1902) wrote that “...contrary to the prevailing notion, all species of *Galaxias* are not confined to fresh-water, and the fact of some living in both the sea and in rivers suffices to explain the curious distribution of the genus.... It is hoped...that students of the geographical distribution of animals will be furnished with a clue to a problem that has often been discussed on insufficient data.” He would later add (Boulenger 1905: 414) that “the key to their mode of dispersal is, with few exceptions to be found in their hydrography...the systematic study of the aquatic animals affords scope for conclusions having a direct bearing on the physical geology of the near past...connecting land areas have been too freely postulated to account for the resemblances between the fishes of Africa and tropical America and Antarctic continents devised to explain the presence of *Galaxias* in Africa.” Moreover, he wrote that “...it is highly desirable that zoologists should base their theories of geographic distribution on geological data. I think we must regret that growing tendency to appeal to former extensions of land or sea without sufficient evidence, or even contrary to evidence in order to explain away the riddles that offer themselves.” Boulenger was clearly sceptical about some of the hypothetical land bridges and continental land masses that were being touted at that time.

It was soon afterwards, in 1904, that McKenzie, in New Zealand, first described the spawning behaviour of *Gl. maculatus*, showing that it does not migrate to sea to spawn but, rather, that the adults move downstream into tidal estuaries to do so, and that the young hatch and it is these that go to sea. Because McKenzie’s account appeared in a very obscure, local, New Zealand magazine, it attracted very little attention and long remained largely unknown there, or more widely around the world of fisheries biology and ichthyology. In the end, from a biogeographical perspective, it doesn’t make a lot of difference whether spawning is estuarine or marine, as the key point is that the larvae do end up in the ocean, so are salt tolerant, are somewhat at the mercy of ocean currents, and their broad marine dispersion is likely. We now know that they spend up to 6 months there, before returning to fresh water to feed and grow to maturity (McDowall and Eldon 1980; McDowall 1990; McDowall et al. 1994).

Another British Museum ichthyologist C. Tate Regan (1905) considered that “The Galaxiidae present many analogies to the Salmonidae of the Northern Hemisphere, both being circumpolar groups of marine origin which are establishing themselves in fresh-water. In both families we meet with non-migratory forms

which appear to have finally left the sea, and with others which return to the sea periodically. But whilst the migratory Salmonidae are anadromous, the migratory Galaxiidae, on the contrary, are catadromous". He concluded (p. 364) that "So long as they were supposed to be a fresh-water group, the geographical distribution of the Galaxiidae was considered to be of considerable interest, occurring as they do in the southern half of Australia, Tasmania, New Zealand and the neighbouring islands, Chile, Patagonia and the Falkland Islands, and at the Cape of Good Hope" (Fig. 8.1). Regan, however, discussed diverse knowledge that various galaxiids were known to spend time in the sea, the unstated implication of his account being that this deprived galaxiids of much of the biogeographical significance of their very broad geographical range, much as had been earlier discussed by Darwin and Boulenger. Regan listed several cases of *Galaxias* ostensibly taken from the sea, including instances reported by Philippi in Chile, Vallentin at the Falkland Islands (discussed above), as well as the observations of Johnston in Tasmania, and of Hutton and Clarke in New Zealand that "...*Galaxias attenuatus* [= *Gl. maculatus*] descends to the sea periodically to spawn." He also perpetuated the error of Hutton's listing of a species from the Auckland Islands (*Gl. bollansi* = *Gl. brevipinnis* – McDowall 1970b) as actually a marine species.

Clearly, there was a growing recognition that galaxiid dispersal through the sea around the Southern Ocean was possible, despite the very large distances involved. Australian Edgar Waite (1909: 586), however, concluded that Hutton's Auckland Island specimen did not come from the sea as presumed by some, and asserted that "...we may now safely dismiss the alleged marine habit of *Galaxias brevipinnis* (*bollansi*) as incorrect." (see, however, McDowall 1964b, 1970a, 1990, where it is shown that *Gl. brevipinnis* does have marine-living juveniles – as Clarke 1899 had earlier stated). New Zealander Charles Chilton (1909: 798) concurred with Waite, and argued that, as "...as Mr Geoffrey Smith (1909: 138) has pointed out, the fact that species of Galaxiidae breed in the sea by no means does away with the value of the group in favour of land connections or proves that they can readily cross the wide oceans," though I think he was wrong.

Regan (1905: 290) stated that the "Galaxiidae and Haplochitonidae [sic] are related to, but more specialised than, the Osmeridae or Smelt family of northern seas," an insightful view that has been supported by many modern studies (McDowall 1969; Fink 1984; Johnson and Patterson 1996). Regan (1913: 291) later discussed the habits of galaxiids, observing that "The conclusion that the Galaxiidae are originally marine and are establishing themselves in fresh water is strengthened by their relationship to the Osmeridae; their distribution has little bearing on the former extension of the Antarctic Continent." He made the interesting observation that "only the marine species occur both at the Falkland Islands and on the continent of South America."

Meek (1916: 145–7) commented that "It has been supposed...that this species of *Galaxias* [*Gl. maculatus*] differs profoundly from other species of the genus and all related genera by making a catadromous migration [primarily that it moves downstream to spawn in the sea]. The evidence is very meagre for such a conclusion"; he noted that Australian McCulloch (1915) had observed them

at the mouths of small streams near Sydney and had pointed to the young entering the streams from the sea, though Meek concluded that “The results are not conclusive, however...” Had Meek known the New Zealand literature he might have been much less sceptical, regarding both the downstream migrations of the pre-spawning adults and the upstream migrations of the juveniles from the sea, the latter constituting a well-known, significant artisanal fishery in New Zealand (Hutton 1872; Clarke 1899; McKenzie 1904; McDowall 1984); he also doubted that *Gl. maculatus* went to sea to spawn, though what he thought, beyond that is uncertain.

Despite increasingly frequent comment from the late 1800s and early 1900s that at least some galaxiids spend time at sea, biogeographers continued to argue for the need for continuity of land to explain the family’s broad southern range. Carl Eigenmann, in the United States, had collected galaxiid fishes in Chile, and wrote in 1923: “Part of the oceanic contribution came from the south and is common to Australia, New Zealand, Patagonia and Chili. The point of origin of this element of the fauna is in doubt unless there was a habitable Antarctic continent in which the Galaxiidae, Aplochitonidae and lampreys developed from which they moved north in all directions.” So, clearly, the knowledge that these fish spend time at sea was not enough to convince him of the prospect of transoceanic dispersal. Eigenmann (1928) would later allude to the marine habits of these fish, including the capture of *Gl. maculatus* at the mouths of streams in southern Chile, and from amongst the sea lettuce *Ulva*, a marine, intertidal alga, and he thought the Chilean *Gl. minutus* to be the juveniles of *Gl. maculatus* returning from the sea. He also (Eigenmann 1928) described a species of *Aplochiton* as marine, though it appears not to be. Eigenmann’s species *A. marinus* is a junior synonym of the largely freshwater-living, though probably diadromous *A. taeniatus* (McDowall 1971, 1988).

New Zealand’s William Phillipps (1926) appears to have favoured spread of galaxiids across land routes, writing “Thus it is possible that in the Cretaceous period, when the New Zealand area was much greater, the Galaxiidae which had originated here, then spread to other land masses. But of *Retropinna* and *Prototroctes*, he stated (wrongly) that “Both species appear to spawn in brackish waters...” adding, however, that “...it is quite possible that the young were formerly capable of crossing short oceanic areas.” In fact, both *Retropinna* and *Prototroctes* in Zealand are diadromous (McDowall 1988, 1990).

Australian ichthyologist Gilbert Whitley (1935) initially favoured an origin for the galaxiids “in the cold southern seas” where they subsequently “acquired the habit of entering rivers of adjacent land masses”, though quite what he meant by this is obscure, and what happened to their ostensibly marine ancestor remains undisclosed. The question of a multiple derivation of galaxiid fishes from a marine ancestry around the Southern Hemisphere is explored further, below. Later, however, Whitley (1956) concluded that “...the modern view seems to favour a large Antarctic continent’s existence in pre-Tertiary times. This has regressed leaving patches where *Galaxias* still lingers or perhaps the land masses have shifted their positions to some extent.... Whether the Galaxiidae are as ancient as the times

when the continents drifted apart, as Wegener postulated, cannot be known, but their ancestors may have been.” This was, I think, the first instance in which galaxiid distribution was suggested as perhaps being connected to continental drift and was, of course, long before the discoveries of plate tectonics which gave so much impetus to the acceptance of continental drift in the late 1960s and since. As far as I am aware, Whitley did not reiterate his views on the place of continental drift on galaxiid biogeography in the more modern environment of the acceptance of plate tectonics.

New Zealander Gerald Stokell (1945, 1950, 1953), though untrained as an ichthyologist and essentially an amateur, was one of the most prolific students of the Galaxiidae of his time, and reviewed the problems in galaxiid distribution. He explored the possibilities of transoceanic dispersal, a common marine ancestry of the riverine/freshwater populations across the family’s range, or the availability of suitable land connections, and he concluded (Stokell 1945) that “some form of land connection does seem necessary”, though he was well aware that some galaxiids spent time in the sea. He considered the prospect of drifting continents, and concluded that “what ever form of connection is postulated, it is essential that it should have been maintained until Galaxiidae was evolved” (Stokell 1950). He finally concluded that “...none of the explanations that have been put forward is consistent with the circumstances as they now appear and I wish to say...that I have no satisfactory explanation to offer” (Stokell 1953). This conclusion is interesting, given that Stokell elsewhere argued that the marine life stage of *Gl. maculatus* might last for 18 or even 30 months (Stokell 1955), rather than the 6 months demonstrated by modern studies (McDowall et al. 1994), perhaps thereby giving even more time for very wide oceanic dispersal to happen, though Stokell himself was clearly unconvinced.

8.3 A Developing But Uncertain Consensus About Transoceanic Dispersal of Galaxiids

American ichthyologist George Myers (1938, 1951, 1953) invested substantial effort in exploring the ability of various sorts of freshwater fish to tolerate marine salinities (discussed in Chapter 5: Some essentials of freshwater fish biogeography), and he held quite clear views on the matter – “that the young of some forms are found in the sea is established, and it is probable that marine wandering is the key to the family’s distribution” (Myers 1951), though he had no personal experience with the fish. He thus reverted to the much earlier view of Darwin (1873) and Boulenger (1902) discussed earlier in this chapter.

American palaeontologist and evolutionary biologist, George Simpson (1940: 756) concluded that “There are also animals...that normally live in fresh water or on land, but that are capable of prolonged sojourn in the sea and are therefore capable of being carried across the ocean without a land bridge. Some of the best instances of southern disjunctive distribution [he thought] belong to this class, for

example the fish *Galaxias*...”, though he had no personal experience with the group. He (Simpson 1940: 758–9) then presented discussion of the possible role of Antarctica in mediating the widespread southern distribution of animals and plants and, commenting on *Galaxias*, cited Regan’s (1905) account that it “freely enters salt water and can live in it indefinitely, that it is probably of marine ancestry, and that it therefore gives no evidence of land connections. This is excellent authority, and this has been shared by a consensus of ichthyologists ever since. Nevertheless *Galaxias* is usually cited by adherents of Antarctic bridges as evidence for their view. So far as any reason can be given for this disregard of authority and consensus, it can be found in the fact that there is a partially conflicting authority, that of Eigenmann (1909) who agreed that *Galaxias* might migrate by marine routes but held this to be highly improbable. This sort of judgement of probability occurs again and again in dealing with the present problem [of the place of Antarctica as a faunal migration route] and so merits further comment....”

Simpson thought it “indeed ‘highly improbable’ that a given fish (or pair) should cross an ocean and colonize waters on the other side at any given time. The chances of occurrence (at a single trial) are extremely small, but probability does not depend solely on *chances* of occurrences, but also on *opportunities* for occurrence [my emphasis]. The chances of throwing five aces with five dice in one throw are negligible, but if the opportunities for occurrence are increased, for instance, by throwing one hundred dice instead of five, or by throwing ten thousand times instead of once, this ‘highly improbable event becomes probable and may even become certain for all practical purposes. So with difficult migrations, such as that of *Galaxias* across the ocean. The great number of individual animals involved, usually thousands or millions, and the long span of time involved, often millions of years, gives so many opportunities for occurrence that the ‘improbable’ event becomes highly probable as long as the basic chance is real and finite, as it is granted to be for *Galaxias*. There is never an absolute certainty that the migration will be accomplished, and its time of occurrence is random – peculiarities that have a definite bearing on animal history....”

Simpson thus applied a probabilistic approach to the potential for dispersal. Moreover, Simpson would have had no idea of just how fecund and prolific this little fish is; had he known, rather than writing of millions, he would have been writing of hundreds of millions of them (McDowall and Eldon 1980). Simpson’s probabilistic approach to dispersal, though much criticised (or caricatured) by some (Croizat et al. 1974), was, I think, correct.

Simpson (1940: 756) also observed that the “whole question of Antarctica as a migration route arises from attempts to explain examples of disjunctive distribution of groups known only, or mainly, from the Southern Hemisphere [on the basis that]...types of land plants and animals do occur in two or more southern regions... and appear to be more closely related to each other than they are to plants and animals of other (i.e. northern) origins. He did not accept the concept of continental drift, as was generally true of scientists in the 1940s, and in commenting (p. 755) that “New facts might break this stalemate [over the potential for southern land

connections implicating Antarctic] at any time”, he was not, I believe, thinking of Gondwana.

Biogeographer de Beaufort (1951: 154) described the very wide geographical range of the family Galaxiidae, and concluded that they are “not strictly freshwater fishes, as some at least of them go down to the sea to spawn”, though it had long before been shown that this is not so (McKenzie 1904; Phillipps 1919; Hefford 1931a, b, 1932). But de Beaufort concluded that “hence dispersal through the sea is not improbable”. He did however, regard *Aplochiton* and *Prototroctes* as being “confined to fresh water” (he was wrong), but cautioned that “it would be hazardous to lay too much stress on their distribution, considering the habits of the related Galaxiidae” [sic], so he was well aware of the group’s potential for transoceanic dispersal, like Darwin and Boulenger, long before him.

In New Zealand, fisheries biologist K Radway Allen (1956), recognised that some galaxiids do spend time at sea, and like some before him, he favoured an explanation of the range of the Galaxiidae based on a shared marine ancestry, though he questioned how one species, like *Gl. maculatus*, could have attained its wide range, unless ancestral to the whole family. Nor did he explain what happened to the shared marine ancestor. He thought that this posed intriguing problems for solution, and seemed generally unaware of their potential scope for dispersal, despite being well familiar with the life at sea of at least this one species. At that time the marine whitebait juveniles of the four other species were not generally recognised, despite reference to them by Clarke (1899).

American parasitologist, Harold Manter (1955: 67), who had some experience of galaxiids, as he worked briefly in New Zealand, argued that the “discontinuous distribution of the genus [*Galaxias*] has long been of interest”, and concluded (p. 68) that “Parasites of *Galaxias* suggest a Pacific and a marine or brackish water origin,” but took the matter no further. And in a general ichthyological text book, American ichthyologist Karl Lagler (Lagler et al. 1962) told how “The principal marine groups represented in the rivers of Australia are...smelt (*Retropinna*)...galaxiids (Galaxiidae)”, the implication being that life at sea was possible, and I think this viewpoint began to gradually achieve widespread acceptance through the 1960s and beyond.

Noted American biogeographer Philip Darlington (1957: 107) concluded that: “The family was once supposed to be confined to fresh water, and all the species probably occur there, but it has long been known that some of them enter or even breed in the sea. One species, *Galaxias attenuatus* [= *Gl. maculatus*], which breeds in the sea [sic], occurs in fresh water with only slight differentiation of races in southern Australia, New Zealand, and southern South America”. Darlington provided no explicit source for his information, though he listed several references, generally. Darlington (1957, 1965) classed galaxiids as ‘peripheral’ freshwater fishes, i.e. those groups not tightly locked into life in fresh water, and he argued for dispersal through the sea. He (Darlington 1957: 107) listed Aplochitonidae as “fresh water but with some species entering or breeding in the sea), and Retropinnidae as having “some living in fresh and others in salt water, but all apparently breeding in fresh water, thus reversing the cycle of the galaxiids.” He later

wrote (Darlington 1965: 109) that the “vertebrate fauna of South Africa includes one representative of a truly southern cold-temperate group, a galaxiid fish which lives in fresh water but probably came through the sea.”

So, by the early 1960s there was, I think, a fairly wide and increasing consensus that Myers (1938, 1949, 1951) had been correct, that the family’s distribution can be explained by transoceanic marine wandering (Darlington 1957, 1965; Caughley 1964; Keast 1968, 1971; Bañarescu 1968, 1970; Gaskin 1970; Corro 1964); among these authors were several who had also accepted the place of Gondwana and continental drift, so that it cannot be argued that they discussed marine wandering as an explicit alternative to drift – but rather that they recognised that both had taken place or might have been influential, but that marine wandering was the key to the range of the Galaxiidae. Darlington’s reference to the South African galaxiid, mentioned in the previous paragraph is somewhat ironically, for if there is any section of the family Galaxiidae whose contemporary distribution might have been influenced by the former presence of a united Gondwana, it was probably the African *Galaxias* that Darlington (1965) had attributed to marine dispersal. The African species may be connected to certain Patagonian species, and perhaps some others, though this question has not yet been addressed seriously.

8.4 Growing Understanding of Galaxiid Ecology and Life History

In the meantime, during the 1960s there was growing knowledge of the role of life at sea (diadromy) among the Galaxiidae. This was not a new idea, as discussed in previous sections of this chapter. For much of recorded history in New Zealand, it was thought probable that only a single species, now known as *Gl. maculatus* was involved in the ‘whitebait fishery’ that harvested galaxiids in such vast numbers as they migrated into the country’s river mouths from the sea (though see Clarke 1899). Noted, early colonial New Zealand, James Hector (1903), had stated, apparently unequivocally and with all the authority of New Zealand’s foremost scientist of the time, that “the question of the true identity of the so-called New Zealand whitebait has been so fully worked out and published that it is hardly necessary to say more about it...*G. attenuatus* [= *Gl. maculatus*] is the adult form of the true whitebait of New Zealand”. However, Hector had apparently not read or understood Clarke’s (1899) observations, in which the latter broached the prospect that other *Galaxias* species, particularly *Gl. brevipinnis*, was implicated in the migrations and that the fishery is also based on them, as well. Later studies have added *Gl. fasciatus*, *Gl. argenteus* and *Gl. postvectis* to the list of species taken in the New Zealand fishery (McDowall 1964b, 1966, 1968a, 1970a, 1984, 1988, 1990; McDowall and Eldon 1980) and so it transpires that there are in fact five diadromous *Galaxias* species in New Zealand (McDowall 1964b, 1990), and so five species that undergo their early development at sea. Moreover, four species are also involved in a similar fishery in Australia – two of those that are also in New Zealand (*Gl. maculatus* and

Gl. brevipinnis), as well as the Australian endemic *Gl. truttaceus* (Blackburn 1950; Fulton and Pavuk 1988; McDowall and Fulton 1996); added to these, rather astonishingly, is the Tasmanian species of the galaxiid genus *Neochanna* in Australia, *N. cleaveri*, which also has marine larvae and juveniles that are taken in the Tasmanian fishery (Fulton 1986).

Thus across more than a century there had been a growing appreciation that a significant number of galaxiid fishes spend a period of at least several months in the sea as a routine phase in the life of each individual fish (McDowall et al. 1994), and in at least seven species, with three of those in Australia, five in New Zealand and one in Patagonian South America. These findings just add to the likelihood that transoceanic dispersal of these fishes, and in a review of the biogeography of the New Zealand freshwater fish fauna (McDowall 1964a), I made a case for that fauna to have largely dispersal origins, not just for the galaxiids, but for all families in the fauna (and I have reiterated this view frequently since that time (see McDowall 1969, 1978, 1984, 1988, 1990, 2002, 1970a).

8.5 New Approaches to Biogeography and the Writing of Donn Rosen

There seemed relatively little residual debate about this question of galaxiid dispersal in the 1960s and early 1970s. Even though it was becoming increasingly recognised that the world's continents had shifted substantially across geological history, the existence of continental drift was not used as an explanation for galaxiid biogeography. Then, in the mid-1970s, there was a distinct methodological revolution in the approach to biogeography.

1. Plate tectonics was rapidly gaining widespread acceptance.
2. Several American ichthyologists (largely) sought to get general recognition of the biogeographic studies of the Italian Leon Croizat (Nelson 1969; Croizat et al. 1974; Rosen 1974a, b, 1978).
3. There was a move towards phylogenetic systematics and the cladistic approach of German Willi Hennig to understanding phylogenetic relationships, substantially stimulated by the publication of an English translation of his German edition (Hennig 1966, and see Brundin 1965, 1966).
4. Some biologists discovered Karl Popper (see Popper 1968) and attempted to make biogeography a more rigorous discipline (perhaps best seen in the writings of Canadian turbellarian systematist, Ian Ball, 1975, 1983).

From the perspective of the biogeography of the galaxiid fishes, significant changes in perspective were propelled by a paper by American Museum ichthyologist Donn Rosen (1974a). This was ostensibly a paper that attempted to clarify the phylogenetic relationships of the strange little Western Australian fish species *Lepidogalaxias salamandroides* (see Fig. 1.2). However, attached to the back of Rosen's paper, as

a kind of addendum, was a long, distinctly polemic attack on the then current status of galaxiid biogeography, as largely reflected in a series of my papers (McDowall 1964a, b, 1968a, 1969, 1970a, b).

In essence, Rosen attempted to discredit a substantial body of work on galaxiid ecology, and in particular to reject the contention that galaxiid biogeography had been driven by the fact that five New Zealand species of *Galaxias* are diadromous and spend their larval and early juvenile life at sea, with *Gl. maculatus*, as discussed above, present across a very broad range, from Western Australia to Patagonian Argentina and the Falkland Islands, making it one of the most widespread ‘freshwater’ fishes known (McDowall 1972, 1970; Waters and Burridge 1999; Waters et al. 2000a). Also, it had been recognised that *Gl. brevipinnis* was present in both Australia (including Tasmania) and New Zealand (including the Chatham, Auckland and Campbell Islands – McDowall 1970b) and so had a quite broad geographical range for an ostensibly ‘freshwater’ fish.

It became almost as though none of this work counted for anything as far as Rosen was concerned, and, moreover, that the prolonged discussions of the place of life at sea in *Gl. maculatus*, that really dated back as far as the work of Darwin (1873), had never taken place. This work was consigned to history as essentially fallacious. Rosen seems to have preferred his intuitions to the data of others working with the fishes.

Several controversies developed that to some extent continue to the present day. Rosen (1974a) pointed out that Stokell (1955) had stated that *Gl. maculatus* was the only galaxiid that he knew to have a marine life stage [though Rosen himself seemed to doubt even that], though what Stokell knew in 1955 was scarcely the last word on the subject in the 1960s and 1970s (McDowall 1964a, b, 1966, 1968a). Moreover, Stokell (1955) had himself, somewhat tentatively, recognised that the juveniles of *Gl. brevipinnis* were sometimes taken with the whitebait [of *Gl. maculatus*] in the river estuaries and, he had concluded, they “might even enter the sea,” perhaps recognising the early observations of Clarke (1899). Similarly, in Australia, Blackburn (1950) had shown that the juveniles of *Gl. truttaceus* and *Gl. maculatus* enter Tasmanian rivers from the sea among the Tasmanian whitebait catch and Scott et al. (1974) confirmed this for what he referred to as *Gl. weedoni* (= *Gl. brevipinnis*).

These observations evidently meant nothing to Rosen (1974a) who actually went as far as questioning whether *any* galaxiids actually occur in the sea at all, though he had no personal experience with the fish, and despite all of the published history (discussed above). He also questioned whether, if they do go to sea (it seems ‘hedging his bets’!), what impact that might have on galaxiid zoogeography, anyway. Thus, Rosen (1974a) chose to throw doubt on the place of marine life in these fishes, despite it having been known to Darwin in the 1870s, being reported by Boulenger in the early 1900s, and discussed repeatedly since by a plethora of other biologists. I can only attribute this to Rosen’s a priori commitment to vicariance and plate tectonics as the only appropriate mechanism for generating the broad Southern Hemisphere range of the Galaxiidae and his sense of urgency to ‘rescue’ galaxiid biogeography from dispersalism. He (Rosen 1974a: 315) adopted an a priori position that “...the galaxiid distribution occupies all the major components of the

original Gondwana land mass except Antarctica and India, and may therefore be at least 90 million years old.”

Perhaps it was the idea of galaxiids living at sea that threatened Rosen’s panbiogeographic agenda. He suggested that I had viewed the “...austral distributions of galaxiids largely from an ecological standpoint...[but went on to argue that] “there is as yet no evidence that any galaxiid does undertake, or is capable of undertaking major, transoceanic migrations. Indeed, no such evidence exists even in the case of the many species that occur in New Zealand which except for *Gl. maculatus*, are confined to New Zealand,” this last comment being simply erroneous, as it had already been recognised that *Gl. brevipinnis* is present in both southern Australia/Tasmania, New Zealand, the Chathams, and New Zealand’s sub-Antarctic islands as noted above (and see McDowall 1970a, b). One can but wonder what kind of ‘evidence’ Rosen would have needed for him to accept that these galaxiids did spend time at sea. Moreover, as far as I am aware no one has proposed that it was ‘migrations’ in the strict sense of the word that had generated the broad range of the galaxiid fishes – rather, it was seen as a matter of dispersal.

Rosen (1974a: 316) asked “How many invasions of the sea are required to account for the widely distributed galaxiids? One, two or a hundred?” The intent and purpose of this presumably rhetorical question, are not clear, and the question itself is ambiguous. At one scale, the number of ‘invasions’ probably amounts to hundreds of millions of larvae, each year, across history, as the progeny of spawning by seven galaxiids move to sea, following spawning and hatch each autumn and winter, and which support the estuary fishery on their return to coastal rivers of southern Australia, Tasmania, New Zealand and Chile (Blackburn 1950; McDowall 1964b, 1968a, 1984; Fulton and Pavuk 1988; McDowall and Eldon 1980; Campos 1973; Mardones et al. 2008).

The scope and scale of these migrations need to be understood. Ever since the European settlement of New Zealand beginning in the mid nineteenth century, it had been well recognised that during the spring the juveniles of species of *Galaxias* migrate into rivers from the sea in prodigious numbers, and for 150 years they had been harvested at the mouths and in the estuaries of river systems all around New Zealand by Caucasian colonial settlers (Powell 1870; Hector 1872; Hutton 1872; Reid 1886; Graham 1953; McDowall 1964b, 1966, 1984) – as well as across centuries by New Zealand’s Polynesian Maori people. The seasonal abundance of these fish can be imagined from Graham’s (1953: 120) description: “Day after day, week after week, during the spring months, shoals of these small fish pursued their way up the rivers.... They were fed to the fowls and ducks until the eggs had a fishy taste. I can remember my father using whitebait as garden manure, the supply exceeded the demand.” Or as Clarke (1899) put it: “The extent of the shoals... in the South Island west coast rivers at times was incredible. Often I have seen the surface of...gardens...for several acres in extent covered some inches in depth with these fry”.

Graham (1953: 120) mentioned an ostensibly “record” catch of 240 pounds in a day” (ca. 150,000 fish) in 1925. However, catches of this magnitude were relatively common in the early years of the fishery, and still happen occasionally, even today,

despite substantial historical decline in the fishery (McDowall and Eldon 1980; McDowall 1984). A catch of >800 kg was recorded as recently as 1977 by one fisherman on one day, i.e. about 1.5 million fish in one small river which consistently produces a catch of about 15,000 kg per season, or about 30 million fish. The greatest catch on record in one day by one fisherman, some time in the 1930s and anywhere in New Zealand, was about 2,000 kg, or about four million fish taken from the Waita River, in South Westland. There are records of one fisherman who in his career caught 104 t of these little fish in a small river that you can easily walk across. These vast numbers of fish are simply not present in the rivers themselves – they enter them from the sea during the southern spring, and can sometimes be watched doing so in vast sometimes seemingly endless shoals. Fishermen catch them in big, fine-meshed nets from the oceanic surf at river mouths. Though Rosen can argue that exactly what the fish are doing at sea, and where, is not known in detail, but this does not alter the fact that they enter river estuaries from the sea all around New Zealand in their hundreds of millions, every year. There are similar, if rather lesser fisheries in Victoria and Tasmania, in Australia, and in southern Chile. Migration is a pulsed phenomenon, peaking as the lunar tide rises, each day (McDowall and Eldon 1980) and catches of several million fish per day from quite small rivers, are not regarded as exceptional across the history of the fishery (McDowall 1968a, b, 1984; McDowall and Eldon 1980). Rosen clearly had no idea what takes place in this fishery, and chose to try to discredit what had been written about it, basing his own, substantial, uninformed ignorance, on his personal intuitions, despite the plentiful published literature.

I suspect that the real question that Rosen may have wanted answered is: “How many times does there need to have been transoceanic dispersal to explain existing distribution patterns of galaxiid fishes?” The answer to this question relates to the broad geographical range of the family and is probably:

- At least three times between Australia and New Zealand (to account for the presence of *Gl. maculatus*, *Gl. brevipinnis*, and the genus *Neochanna* in both countries)
- Once at least, probably from Australia, to Lord Howe Island to account for the presence there of *Gl. maculatus*
- At least once, probably from New Zealand to the N Z sub-Antarctic islands, to account *Gl. brevipinnis* on these islands
- Five times from New Zealand to the Chatham Islands to account for the occurrence there of four diadromous galaxiids and an endemic Chathams’ species of *Neochanna* bearing in mind that the Chatham Islands probably emerged from the sea only a few million years ago
- Once from either Australia or New Zealand to Patagonian South America
- And once from Patagonia to the Falkland Islands
- The latter dispersals both to account for the presence there of *Gl. maculatus*

When viewed in such skeletal detail, we are looking at a substantial amount of dispersal across sometimes very wide ocean gaps around the Southern Ocean, and this is not something to assume lightly.

Rosen (1974a: 317) objected that “the number and types of historical events that must be assumed to account for McDowall’s hypotheses of galaxiid distributions renders the hypotheses untestable”, and it seems curious that it is the *number* of hypotheses that is charged with being untestable. Rosen concludes that we should, therefore give “serious consideration of the concept that:

1. Galaxiids are where they have been for a very long time.
2. That some of the principal lineages of galaxiids have been evolving in parallel on the different land masses.
3. That a Gondwanaland hypothesis simply accounts for the now disparate galaxiid population centres.

How such a scheme can be described as simple is unexplained. An ancient vicariant origin for the distribution of the Galaxiidae, as insisted by Rosen does, for instance, require that stocks of *Gl. maculatus*, present on Australia, Tasmania, Lord Howe Island, the Chatham Islands, Patagonian South America and the Falkland Islands should have remained morphologically undifferentiated for >80 million years (fish from the various areas are morphologically indistinguishable to me – McDowall 1972). Is that ‘simple’? It is, of course, not impossible, if the apparent morphological stasis of New Zealand’s relictual rhynchocephalian tuatara, genus *Sphenodon* (a ‘living fossil’) is evidence. One of the curious aspects of Rosen’s position, is that he rejects dispersal hypotheses because they are untestable. He lacked the modern luxury of molecular DNA sequencing analyses which are showing that the separation of the stocks across this vast range is substantially more recent than he assumed (Waters and BurrIDGE 1999; Waters et al. 2000a). In the end, Rosen (p. 321) concludes that Leon Croizat’s (1958) “concept of ‘tracks’ forms the only scientific basis for biogeographic analysis because it allows an interpretation of the history of the distribution of one group to be tested by those of others without resort to surmise”, though the nature of the ‘test’ is elusive. Rosen (p. 321) stated that his “purpose...[was] to emphasize that conclusions concerning the distribution, dispersal and phylogeny of galaxiid fishes need not exceed the evidence presently available”, but spent several pages refuting the evidence that was available.

It is, of course, not inevitable that the entire range of the family has been driven by dispersal, and it does look, from phylogeographic studies (BurrIDGE et al. 2009) that there may have been some quite ancient distributions not involving diadromous stocks of galaxiids, e.g. the Chilean *Gl. platei* seems to share a common ancestry with the South African galaxiid lineage; and the Australian *Galaxiella* species complex seems closest to the Patagonian *Brachygalaxias*. None of these is diadromous, nor does any of them seem to be derived from other species that are diadromous. Thus, here, we may be looking at a combination of dispersal and vicariance processes across the breadth of the family as a whole (McDowall 1990). These are interesting questions, and further study is needed.

Rosen (p. 317) also attempted to cast doubt on observations that other, galaxiid-related taxa are also diadromous, such as the Tasmanian *Lovettia*, despite this fish being anadromous and supporting a well-documented river mouth fishery (Blackburn 1950). He expressed surprise that, if it is anadromous, that *Lovettia* “is

confined to Tasmania, not even reaching the nearby Flinders and Cape Barren Islands, an odd behavior for a type of fish that, according to McDowall, goes to sea” (and it does – Blackburn 1950; McDowall 1988). This is a curiously contorted argument, and it seems strange that absence of a species on certain islands is used to refute observed diadromous behaviours of that species elsewhere. Interestingly, *Lovettia* has recently been recorded from mainland Australia (Raadik 2008), and Rosen could not have known that. However, it is uncertain whether knowledge of its presence on the Australian mainland derives from more thorough sampling there, or is a result of a recent dispersal event northwards across Bass Strait between southern Victoria, Australia, and Tasmania.

Thus, in the end, Rosen (1974a: 322) found himself unwilling to credit research results of other researchers demonstrating the return migrations of a number of New Zealand *Galaxias* species from the sea, concluding “...it is still a question as to *what exactly occurs in the sea and where...*” (present author’s emphasis). He is, of course correct: we do not know “*exactly what occurs in the sea and where*”, but that of course is a quite different question from whether or not these fish spend time at sea, as they do, and have been taken in plankton nets at least 700 km from the nearest land (McDowall et al. 1975). Rosen, of course, did not know that, though such findings confirm earlier assertions of the presence of these species at sea.

It is perhaps curious that Rosen seems to have had no problems accepting that species of osmerid smelt, which are relatively closely related to galaxiids (McDowall 1969; Fink 1984; Johnson and Patterson 1996), have marine life stages, nor, for that matter, the even more closely related southern retropinnid smelts also spend time at sea, but he rejected this for galaxiids (McDowall 1988, 1990).

8.6 Do Galaxiids Breed in the Sea?

Some early assertions suggested that some galaxiid spawn at sea, but this is incorrect, and although it has long been known no galaxiid spawns in the sea, some persist in saying they do, even in the modern literature, ironically including the writing of Rosen himself (Breder and Rosen 1966; also McLean 1974; Bond 1979), but Rosen (1974a) had apparently forgotten this.

Reports of galaxiids spawning at sea seem to stem from observations of huge shoals of ripe adults of inanga, *Gl. maculatus* streaming downstream into river estuaries in the autumn, something that was well known to New Zealand’s Polynesian Maori, who used to harvest them in large quantities (McDowall 1990; *in press*). Rosen (1974a: 321) pointed out that some non-estuarine spawning sites are known, but it is long- and well-authenticated that this species spawns during the autumn in tidal estuaries, in locations typically a little upstream of the salt wedge that pushes upstream into river estuaries on rising spring tides during the particularly high tides that accompany the new and/or full moons (McKenzie 1904; Phillipps 1919; Hefford 1931a, b, 1932; Burnet 1965; Benzie 1968; McDowall 1968a, 1990). Observations that spawning is sometimes not estuarine, and in

particular that it takes place sometimes in freshwater lakes, do not refute the existence of (typical) tidal spawning sites, but simply show that the species is facultative and in some instances reproduces in waters not influenced by tidal fluctuations. Equally, Pollard's (1971) observations of spawning of a landlocked stock of *Gl. maculatus* in a lake tributary in Australia, after an upstream migration, does not refute the general truth that spawning is usually preceded by a downstream migration.

Curiously, Rosen (1974a: 315) claimed that *Gl. maculatus* is described as anadromous when it is marginally catadromous (McDowall 1968a, b, 1988, 1990), and Rosen was clearly unfamiliar with the literature on the species he was discussing with such apparent authority and finality. Moreover, he had, himself, previously ranked this species catadromous (Breder and Rosen 1966), stating that the young are "presumed to be washed out to sea for a period of growth before returning to fresh water to breed (as in the northern salmonids); the return migration to fresh water is not a breeding migration, but a trophic one. The juveniles do not mature for many months, thereafter."

At first entry into rivers from the sea in the New Zealand, Tasmanian, and also Chilean fisheries for this fish, the juvenile, 'whitebait' galaxiids, as taken in the fishery, are completely translucent, as is widely true of animals living in the marine plankton. Within a few days of entry to fresh water, as they begin to feed on freshwater organisms, they develop body pigmentation (McDowall 1968a, 1990; McDowall and Eldon 1980), and that process, too, is consistent with the marine/freshwater biome shift that is recognised.

Rosen (p. 322) also stated that "It is assumed, [Rosen's original emphasis] in other words, based on incomplete knowledge of *G. maculatus*, that larval galaxiids are to be found periodically in the stretches of ocean between Australia and New Zealand, New Zealand and South America, and South America and Africa, or that larvae could have been there in the past". What Rosen meant by "periodically" in this context is unclear, but as pointed out above galaxiids have certainly been taken at sea, up to 700 km from New Zealand, in some oceanic plankton sampling. Once more, Rosen would not have known this in the early 1970s, though these recent results do show that what was observed at that earlier time was correct, despite his scepticism.

The 'uniformity of phenotype' of *Gl. maculatus*, even if this should prove to be ultimately attributable to transoceanic dispersal, applies now and has always applied to other galaxiids. As subsequent studies on galaxiid ecology have shown (McDowall et al. 1975; Hickford and Schiel 2003; Ruttenberg et al. 2005; Hale and Swearer 2008; Hale et al. 2008; Rowe and Kelly 2009), based on catches at sea and otolith microchemistry, life at sea does happen in some galaxiids.

As well, based on sequencing of DNA, it is evident that gene flow across the ranges of some galaxiids has clearly been much more recent than the separation of New Zealand from Gondwana >80 Ma. The molecular studies of *Gl. maculatus* (Waters and Burridge 1999; Waters et al. 2000a) suggesting that there has been dispersal of this species around the Southern Ocean much more recently than could have been associated with a united Gondwana. Similarly, other results suggest that the most recent gene flow between the Australian mudfish and New Zealand

members of *Neochanna* may have been only 10 million years ago (Waters and White 1997; Waters and McDowall 2005), which is also far too recent for the Australia-New Zealand connection in *Neochanna* to date back to New Zealand's connection to Gondwana (Cooper and Millener 1993; McLoughlin 2001).

Everything we know about the diadromous galaxiids points to, or is consistent with, their occurrence in and migration from the sea. Rosen, of course, did not have access to some of these studies, but they do confirm the conclusions in the 1960s and 1970s. Rosen's knowledge of the time was inadequate, his arguments flawed, and his conclusions erroneous. Galaxiid fishes have dispersed around the Southern Ocean much more recently than 80 mya, when New Zealand detached from Gondwana.

8.7 *Galaxias maculatus* in Chile

Chilean biologist Hugo Campos (1973) also explored some of these issues, based on his experience with *Gl. maculatus*. Campos made the curious argument that the ecology of *Gl. maculatus* "reveals a strong bond with limnic waters which does not permit long residence in the oceans. If it was dispersed across oceans by currents from the west winds, its complete cycle of post-embryonic development ought to have adapted to the sea or the fish would die, and subsequently by means of convergence, the populations on each continent would have acquired a migratory behaviour in the estuaries. This seems to be wholly improbable since the whitebait migrate to fresh water where they become adults and they live mainly in the rivers paying only occasional visits to the estuary for hatching. Finally, no galaxiids totally adapted for the sea are known." This argument seems totally unfathomable. Campos (1973) told of finding specimens in an enclosed bay where salinities were $\approx 20\%$, and seems to have assumed that they go no further to sea – though he gives no evidence of having looked any further. What is required is that some life history stage be able to live in the sea for long enough to permit the dispersal required to achieve the existing distribution, and for enough fish to do so to establish a founder population. The dispersal distances are great, and it no doubt exceedingly rarely happens, but it only needs to happen once for each geographical disjunction, involving populations in Australia, Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, Patagonian South America and the Falkland Islands (McDowall 1972).

Campos (1984: 113) later took the view that "Both ecological and systematic [taxonomic] data are important in resolving what has become a controversial topic among the students of biogeography". He argued that "the estuarine phase in galaxioids is not a true marine dispersive phase", but what he meant by that he did not explain, nor how he knew is unstated. The greatest controversy involves explaining "how the known zoogeographic patterns and the phylogenetic relationships of galaxioids were formed." So we seem to be dealing quite generally, with limits imposed by personal scepticism (by both Rosen and Campos), and unrelated to any evidence. It is essentially 'the argument from personal incredulity'.

Campos thought that “The theory can be separated into ecological (i.e. via dispersion) versus historical (i.e. vicariant events)... The ecological theories present oceanic dispersion as the principal mechanism. Some proponents of marine dispersion also suppose that galaxioids had marine ancestors, that they travel long distances to reach new habitats, and that some species can reproduce in the sea.... The majority of these authors lacked reliable knowledge about galaxioid distributions,” (p. 121) and, again, this seems unfathomable. So, Campos (p. 122) disclaimed “belief in transoceanic dispersal of galaxioids.... I do not think that there is a marine phase in a strict sense, but rather an estuarine phase that reproduces in saltwater, with the juveniles feeding near the coast before entering rivers.” Though he does not say so, Campos seems to be assuming the existence of an ancestral, presumably Pangaean distribution for both the northern salmonid/osmerid lineages and the southern galaxioid lineages. How this helps, us to understand galaxiid biogeography is unclear. He concluded that “It would seem that the historical rather than dispersal explanation provides greater insight into the origin of the families in different ancestral groups of the Northern Hemisphere”. (p. 121) and added: “My studies...have led me to conclude that the best explanation for the disjoint distribution of the galaxioid fishes...is the disruption of the hypothetical continent of Gondwana.... Within a general Gondwana distribution, the galaxioids are merely a part of a pattern, and this makes the search for the historical rather than the ecological exploration more interesting” (p. 123). There seems no way to refute an argument like that? But, above all else, all ecology is ultimately history, and all history is a product of ecology; they are the same processes viewed at different spatial and temporal scales.

8.8 Rosen on the Biogeography of Darlington

Rosen (1974a: 321) was also severely critical of Darlington (1965), of whom he wrote: “Darlington, in fact, dismissed three of the most outstanding examples of correspondence of transantarctic biological distributions with a Gondwana hypothesis (galaxiids, chironomid midges and southern beeches) simply by invoking any and all conceivable means of dispersal. Croizat (1958) has termed this ecological dispersive approach ‘zoogeography by apriorisms’, a view which I entirely concur.” However, Rosen did not specify the apriorisms he objected to, nor did he detail the apriorisms of his alternative hypotheses, such as the need for morphological stasis enduring for >80 million years. In the end, Rosen apparently also seems to have had ‘second thoughts’ on the matter, stating “My purpose is not so much to support or reject the general concept of Gondwanan distribution or of persisting long-range waif transport as it is to emphasize that conclusions concerning the distribution, dispersal and phylogeny of galaxiid fishes need not exceed the evidence presently available.” But then he reverts to the same arguments about whether or not the fish occur in and/or breed in the sea. Rosen et al. (1974) made a similar plea. But Rosen is really not asking us to reject waif dispersal because

the evidence for it is too meagre; he is asking us to reject it because he disbelieves the published evidence. Equally, he is asking us to accept a Gondwana explanation because he thinks the evidence for that is overwhelming. Rosen's account is not a refutation of waif dispersal so much as a attack on limited aspects of a waif dispersal hypothesis, based on ignorance of the fish involved, and followed by the presentation of an alternative hypothesis, the implications of which are not considered in any way.

Rosen (1974a: 321) accused Darlington (1957) of citing Regan (1905), who, according to Rosen, "offered a set of unsupported statements that galaxiids freely enter the sea and can live indefinitely in salt water and that they give no evidence of land connections." But "indefinitely" was Rosen's word, not Regan's! Nor did Regan make any statement about land connections. Regan (1905) was in fact among six authors cited by Darlington (1957: 107) as "Leading references in this zoogeographically interesting family". And, what Regan did write was "So long as they were supposed to be a fresh-water group, the geographical distribution of the Galaxiidae was considered to be of considerable interest.... The occurrence of *Galaxias maculatus* in the sea has been reported by Valenciennes and by Philippi off the Falklands and off the coast of Chile, respectively. The observations of Johnston in Tasmania and Hutton and Clarke in New Zealand are to the effect that *Gl. attenuatus* [= *Gl. maculatus*] descends to the sea periodically to spawn [though it does not actually spawn at sea]. Mr Rupert Vallentin has seen shoals of little fishes which I identify with the *Galaxias gracillimus* of Canestrini in the sea at the Falkland Islands..." Thus to state as Rosen did, that Regan offered a set of unsupported statements that galaxiids freely enter and can live indefinitely in the sea, and that Darlington (1957, 1965) merely cited such observations, is a caricature of history.

8.9 Does *Galaxias* Occur at Sea (Again)

One of the central questions remains: "Does *Galaxias* occur in the sea?" Despite Rosen's scepticism, the answer is: "Unequivocally, yes." That does not, of course, prove that galaxiids have dispersed around the Southern Ocean between Australia, New Zealand, Patagonian South America and the Falkland Islands, but it does render the claim a little more credible, and there is other information that supports that conclusion. Again, Simpson's (1940, 1952) ideas relating to the possibility of an improbable event taking place, if there is enough time, become relevant, especially when the vast numbers of these fishes in the seas around Australia and New Zealand are understood (discussed on pp. 180–181). At least, it cannot reasonably be argued that the salinity tolerances of some galaxiids are so low, that prolonged life in the sea, and such dispersals, are unthinkable. Specifically, the juveniles of six species of *Galaxias* and one of *Neochanna* do occur in the sea, live there for several months (Blackburn 1950; McDowall et al. 1975, 1994; Fulton 1986; McDowall and Kelly 1999; Rowe and Kelly 2009) and

curiously (or not) the most widespread members of the family are (I think not coincidentally), those that do spend a part of their lives in the sea.

Rosen's appraisal of the studies of galaxiid ecology and biogeography reflects his serious doubts at two levels:

1. Are the ecological data published about galaxiid fishes correct?
2. How should these ecological observations be used in interpreting galaxiid distribution patterns?

Although elements of both questions are implicit in Rosen's discussion, they are neither explicit nor distinguished from one another. And though he spends several pages discussing the correctness of published ecological observations on these fishes, he finally makes a case for ignoring all ecological evidence in considerations of historical biogeography, concluding that this is not relevant. It appears that all that mattered was that distribution patterns conformed to his preconception of the former configuration of Gondwana, its fragmentation, and the place of galaxiid fishes on Gondwana. If Rosen thought that ecology was irrelevant to biogeography, there seems little point in refuting the ecological information!

Rosen began his case with the statement that "the galaxiid distribution occupies all of the major components of the original Gondwana, except Antarctica and India, and may therefore be at least 90 million years old," there was implicit an a priori assumption that the origin and distribution of the galaxiids must be tied up with the fragmentation of Gondwana, to the exclusion of any possibility. In the final analysis, Rosen (1974a: 318) has claimed that oceanic dispersal hypotheses are "vague and untestable, and therefore unrejectable hypotheses so why fuss with whether the fish can/do spend time at sea? Or debate the evidence on how galaxiids are being moved, if they could survive, if the physical details of ocean currents are appropriate, of waif dispersal has occurred sufficiently often?

But, it seems to me that there are other, no less basic, questions relating to Rosen's views on vicariance and Gondwana:

- Do the phylogenetic affinities of galaxiid fishes correlate with the timetable of Gondwanan fragmentation; can we assume widely varying evolutionary rates in various lineages?
- Were galaxiid fishes present on the appropriate parts of Gondwana, and widely enough to be represented on the now widely separated Gondwana fragments?
- Is it possible that both *Galaxias* species in common with widespread ranges and others that are locally endemics could co-occur across the time involved in Gondwanan fragmentation?
- Could widely disjunct conspecific populations remain morphologically indistinguishable for the requisite 80+ million years since Gondwana began to fragment and New Zealand became isolated in the southwestern Pacific?

Rosen writes of Gondwanan distributions and dispersals as if they are so self-evidently true that he sees no need to explore the implications making all his debate about galaxiids a sea irrelevant.

8.10 Another Point of View and Summation

Whereas Rosen began with the assumption that galaxiid distributions are inextricably linked to Gondwana because their distribution is Gondwanan, Goldberg et al. (2008: 3319) neatly presented three scenarios that provide different possible alternative explanations for such distributions:

- A most restrictive view is that a taxon is Gondwanan and has been continuously present in New Zealand since it parted from Gondwana as Rosen assumed.
- The taxon (family) could have had Gondwana origins, but could also have arrived later in New Zealand, especially if New Zealand did sink beneath the sea and then re-emerge during the early-mid Cenozoic, as some are postulating (Landis et al. 2008).
- The taxon may have a distribution that has all the appearances of a Gondwanan origin, but for which a uniform explanation for generating the range does not apply, as might result entirely from dispersal of the taxon around the Southern Ocean, and onto many of the lands thought, once, to have been a part of Gondwana during the Mesozoic.

Clearly, each of these scenarios is possible and needs to be considered. As it happens, the molecular information on *Gl. maculatus* (Waters and Burrige 1999; Waters et al. 2000a) suggest that there has been gene flow in this species across its huge geographical range around the Southern Ocean far more recently than could have any connection to Gondwana, and that therefore *Galaxias* has dispersed. Given that this is true of *Gl. maculatus* we should, I think, accept that it has happened in other parts of the family. Molecular evidence suggests that the most recent gene flow between the Australian mudfish and New Zealand members of *Neochanna* may have been only 10 million years ago (Waters and White 1997; Waters and McDowall 2005), which is, again, far too recent for the Australia-New Zealand connection in *Neochanna* to date back to New Zealand's connection to Gondwana – c.80 million years ago in the case of New Zealand (Cooper and Millener 1993; McLoughlin 2001).

As a part of his argument for a Gondwanan Galaxiidae, Rosen (1974a) argued that the South African galaxiid (it is actually a species complex: Waters and Cambray 1997; McDowall 2001) is the least derived of all galaxiids, ostensibly on grounds that the position of its dorsal fin is less posterior than in other galaxiids. If he was right, the prospect that the South African *Galaxias* form a sister taxon to all other galaxiids would have some interesting implications for galaxiid biogeography. Rosen does not, however, explicitly explain why he regards the less posterior dorsal fin as a primitive character in African galaxiids, but it is presumably because he recognised that one of the distinctive, perhaps derived, characteristics of the family Galaxiidae is the rearward position of its dorsal fin, in contrast with a dorsal fin above the pelvic fins in other lower euteleostean, salmoniform families such as Salmonidae and Osmeridae, which may be closely related to Galaxiidae.

However, Rosen's conclusion on the position of the dorsal fin is erroneous on several distinct grounds. The reason why the dorsal fin appears to be more anterior (or perhaps this is better seen as less posterior) is because the South African galaxiid has a particularly long caudal peduncle, and so it has nothing at all to do with the position of the dorsal fin, itself. The dorsal fin in the South African stocks originates directly above the origin of the anal fin, as it does in virtually all galaxiids, so that in terms of the fish's coelomic cavity, the fin in the African galaxiids is in essentially the same position as in most other galaxiids. Thus the reason why the dorsal fin in the South African galaxiid *appears* to be anterior is actually because the body, posterior to the vent, is relatively long. Moreover, this feature is not unique to the South African *Galaxias*, but is equally true of several New Zealand species (McDowall and Waters 2002, 2003), which also have very long caudal peduncles. And, furthermore, an additional reason why Rosen was incorrect is that if the position of the dorsal fin is a signal for primitiveness in the Galaxiidae, then in the Australian galaxiid genus *Paragalaxias*, the dorsal fin is nearly directly above the pelvic fins, and so in much the same position as in salmonids and osmerids. However, whether this position is primitive for galaxiids, or is a reversion to such a position in *Paragalaxias*, is presently uncertain.

So, when it comes to galaxiid biogeography, Rosen (1974a: 318) makes the point that even though it is possible for insects to be carried away by winds and for fishes to be dispersed by ocean currents, there is no evidence:

1. If or how galaxiids (or midges) are being so moved
2. Whether they could even survive such a journey in terms of what their biology, their ontogenetic requirements or (in the case of fishes) the oceanic ecology would permit
3. Whether the physical details of the ocean currents or winds can be correlated precisely with galaxiid or midge population centres
4. Whether waif transport has occurred the number of times necessary to account for the number of lineages in each population centre, and finally
5. Even if present distributions are relatively recent, whether we can assume that wind and current patterns have not been different during the entire evolutionary histories of the groups (but why their entire evolutionary histories?)

Rosen argued that the "number of separate events that must be assumed in such chance dispersal hypotheses is unknowably large, as against the more manageable framework [in his view, at least] of a changing continental landscape that is being provided by a growing and consistent body of geophysical evidence." But Rosen asked none of the concomitant questions associated with the postulate that galaxiid distribution is associated with that continental landscape, as if an equally large and unknowable events is not then involved, as for instance the need for populations of a widespread species like *Gl. maculatus* to persist without morphological change across its broad range since Gondwanan fragmentation in the late Mesozoic. Rosen accused Darlington of adopting an approach of "zoogeography by apriorisms", but neglected to address the 'apriorisms' of his own.

This controversy continues to some extent amongst some biogeographers, as indicated by sequential editions of a significant book on biogeography. Brown and Gibson (1983) suggest that the southern circumpolar distribution of galaxiids is a result of dispersal. A second edition of this book (Brown and Lomolino 1998) attributed the same pattern to plate tectonics and continental drift without any explanation of the change of view. More curiously, however, in the third edition of this book (Lomolino et al. 2006) there is no mention of this question – galaxiid biogeography is not discussed. I think Brown and Gibson (1983) were right. That does not mean that there has been no impact from Gondwana, and it is possible that some elements in the fauna could reflect such ancient connections (McDowall 1990). However, Lord Howe Island, Campbell and Auckland Islands are relatively young volcanoes; New Caledonia is believed by some to have been submerged by sea into the middle Cenozoic (Grandcolas et al. 2008); the Chathams emerged from the sea probably less than 3 million years ago (Campbell and Hutching 2007; Adams et al. 2008; Campbell et al. 2009); even New Zealand may once have been beneath the sea (Landis et al. 2008); and although the Falkland Islands have freshwater fishes of Patagonian provenance (McDowall 2005), the islands themselves are derived, geologically, from the southeastern corner of South Africa. Clearly dispersal must have been very important for a substantial part of the very wide geographical range of the family Galaxiidae in southern cool-temperate latitudes: galaxiid fishes may occur on lands formerly connected to each as a part of Gondwana, but much of their biogeography does not seem to relate to the fragmentation of Gondwana, itself.

In the final analysis, even though it appears that the geographical distribution of the galaxiid fishes involves lands that were once a part of Gondwana, the modern distribution of the family may have little or nothing to do with Gondwana, in terms of process and historical detail, though we should not entirely ignore the prospect that some lineages did achieve their present range in association with Gondwanan fragmentation. Additional molecular phylogenetic studies are needed to explore patterns of relationships. BurrIDGE et al. (2009: A35) conclude that “The entire New Zealand galaxiid fauna appears to postdate a putative late Oligocene drowning of [the New Zealand] landmass, which may also explain the absence of older lineages of direct derivation from the supercontinent Gondwana. Broadly, the southern distribution of galaxiids reflects a large number of transoceanic dispersal events.”

References

- Adams CJ, Campbell HJ, Griffin WJ (2008) Age and provenance of basement rocks of the Chatham Islands: an outpost of Zealandia. *N Z J Geol Geophys* 51:245–259
- Allen KR (1956) The geography of New Zealand's freshwater fish. *N Z Sci Rev* 14:3–9
- Baker AJ, Huynen LJ, Haddrath O, Miller CD, Lambert DM (2005) Reconstructing the tempo and mode of evolution in an extinct clade of birds with ancient DNA: the giant moas of New Zealand. *Proc Nat Acad Sci* 102:8257–8262
- Ball IR (1975) Nature and formulation of biogeographical hypotheses. *Syst Zool* 24:407–430
- Ball IR (1983) Planarians, plurality and biogeographical explanations. In: *Evolution, time and space: the emergence of the biosphere*. *Syst Ass Spec Publ* 23:409–430

- Bañarescu P (1968) Recent advances in teleost taxonomy and their implications on freshwater zoogeography. *Rev Rom Biol Ser Zool* 13:153–160
- Bañarescu P (1970) Some general zoogeographic problems of peripheral and vicarious freshwater fishes. *Rev Rom Biol Ser Zool* 15:315–322
- Barker NP, Weston PH, Rutschmann F, Sauquet H (2007) Molecular dating of the ‘Gondwanan’ plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *J Biogeogr* 34:2012–2027
- de Beaufort LF (1951) Zoogeography of the land and inland waters. Sidgwick and Jackson, London, 208 pp
- Beddard FE (1895) A textbook of zoogeography. Cambridge University Press, Cambridge, 246 pp
- Benzie V (1968) A consideration of the whitebait stage of *Galaxias maculatus attenuatus* (Jenyns). *Proc N Z Ecol Soc* 2:559–573
- Berg LS (1940) The classification of fishes both Recent and fossil. *Trudy Inst Akad Nauk SSSR* 5: 1–517 (reprint: Edwards Publ. Ann Arbor, Mich., 1947)
- Blackburn M (1950) The Tasmanian whitebait, *Lovettia sealii* (Johnston) and the whitebait fishery. *Aust J Mar Freshwater Res* 2:155–198
- Bond C (1979) The biology of fishes. WB Saunders, Philadelphia, PA, 514 pp
- Boulenger GA (1900) A list of the fishes collected by Mr Rupert Vallentin in the Falkland Islands. *Ann Mag Nat Hist* 7:52–54
- Boulenger GA (1902) The explanation of a remarkable case of geographical distribution among fishes. *Nature* 67:84
- Boulenger GA (1905) The distribution of African fresh-water fishes. *Nature* 72:413–421
- Breder CM, Rosen DE (1966) Modes of reproduction in fishes. Natural History Press, Garden City, NJ, 941 pp
- Briggs JC (2007) Panbiogeography: its origin, metamorphosis and decline. *Russ J Mar Biol* 33:273–277
- Briggs JC (2009) Darwin’s biogeography. *J Biogeogr* 36(6):1011–1017
- Brown JH, Gibson AC (1983) Biogeography. Mosby, St Louis, MO, 643 pp
- Brown JH, Lomolino MV (1998) Biogeography. Sinauer, Amherst, MA, 691 pp
- Brundin L (1965) On the real nature of trans-Antarctic relationships. *Evolution* 19:496–505
- Brundin L (1966) Trans-Antarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagyiidae. *Kung Sven Vetenskap Hand* 11:1–472
- Burnet AMR (1965) Observations on the spawning migrations of *Galaxias attenuatus* (Jenyns). *N Z J Sci* 1:79–87
- Burridge CP, McDowall RM, Craw D, Wilson M, Waters J (2009) Does Gondwanan vicariance explain any aspect of contemporary galaxiid (Euteleostei: Galaxiidae) distribution. 8th Indo-Pac Fish Conf, 2009ASFB Worksh Conf 31 May – 5 June 2009, Fremantle WA, p A34
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Campbell H, Begg J, Beu A, Carter A, Curtis N, Davies G, Emberson R, Given D, Goldberg J, Holt K, Hoernli K, Malahoff A, Mildenhall D, Landis C, Paterson A, Trewick S (2009) Geological considerations relating to the Chatham Islands, mainland New Zealand and the history of New Zealand terrestrial life. *Geology and Genes IV. Geol Soc N Z Misc Publ* 126:5–6
- Campos H (1973) Migration of *Galaxias maculatus* (Jenyns) (Galaxiidae: Pisces) in Valdivia Estuary, Chile. *Hydrobiologia* 43:301–312
- Campos H (1984) Gondwana and neotropical galaxioid fish biogeography. In: Zaret T (ed) *Evolutionary ecology of neotropical freshwater fishes*. Junk, The Hague, The Netherlands, pp 113–125
- Caughley GC (1964) Does the New Zealand vertebrate fauna conform to zoogeographic principles? *Tuatara* 12:49–56

- Chilton C (1909) The biological relations of the sub-Antarctic Islands of New Zealand. In: Chilton C (ed) the sub-Antarctic Islands of New Zealand. Canterbury Philosophical Society, Christchurch, N Z, pp 793–807
- Clarke FE (1899) Notes on New Zealand Galaxiidae, more especially those of the western slopes, with descriptions of new species. Trans Proc N Z Inst 31:78–91
- Cook LG, Crisp MD (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. Proc R Soc Lond B Biol Sci 272:2535–2544
- Cooper A, Mourer-Chauvire C, Chambers GK, von Haeseler A, Wills AC, Paabo S (1992) Independent origin of New Zealand moas and kiwis. Proc Nat Acad Sci 89:8741–8744
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. Trends Ecol Evol 8:429–433
- Corro G del (1964) La Gondwana, el antiguo continente austral. Publ Extens Cult Diad, Mus Arg Cienc Nat ‘Bern Riv’ e Inst Nac Investig Cienc Nat 12:1–90
- Couper RA (1960) Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their palaeogeographic significance. Proc R Soc Lond B Biol Sci 152:491–500
- Croizat L (1958) Panbiogeography – an introductory synthesis of zoogeography, phytogeography and geology: with notes on evolution, systematics, ecology and anthropology, etc. Publ. Author, Caracas, Venezuela, 3 vols
- Croizat L (1964) Space, time, form: the biological synthesis. Publ, Author, Caracas, Venezuela, 881 pp
- Darlington PJ (1957) Zoogeography: the geographical distribution of animals. Wiley, New York, 675 pp
- Darlington PJ (1965) Biogeography of the southern end of the world. Harvard University Press, Cambridge, MA, 236 pp
- Darwin C (1873) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 6th edn. Murray, London, 458 pp
- Darwin C (1896) Journal of Researches into the natural history of the countries visited during the voyage of HMS Beagle round the world. Nelson, London, 615 pp
- David BO, Chadderton L, Closs GF, Barry B, Markwitz A (2004) Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*). Dep Cons Sci Int Ser 160:1–23
- Day F (1888) Supplement to the fishes of India, being a natural history of the fishes known to inhabit the seas and freshwaters of India, Burma and Ceylon. Williams & Norgate, London, pp 779–816
- Eigenmann CH (1909) The freshwater fishes of Patagonia and an examination of the Archiplata-Archihellenis theory. Rep Princeton Univ Exped Patagonia 3:211–374
- Eigenmann CH (1923) Fishes of the Pacific coast of South America and the bearing of their distribution on the history and development of the topography of Peru, Ecuador and western Colombia. Am Nat 57:193–210
- Eigenmann CH (1928) The freshwater fishes of Chile. Mem Nat Acad Sci 22:1–80
- Fink W (1984) Basal euteleosts: relationships. Am Soc Ichthyol Herpetol Spec Publ 1:202–206
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp
- Fulton W (1986) The Tasmanian mudfish, *Galaxias cleaveri*. Fish Sahul 4:150–151
- Fulton W, Pavuk N (1988) The Tasmanian whitebait fishery: summary of present knowledge and outline of future management plans. Tasmanian Inl Fish Comm Occ Rep 88–01:1–27
- Gaskin DE (1970) The origins of the New Zealand fauna and flora: a review. Geog Rev 60:414–434
- Gill T (1893) A comparison of antipodal faunas. Mem Nat Acad Sci 6:91–124
- Gill T (1896) The former northward extension of the Antarctic continent. Nature 53:366
- Goldberg J, Trewick SA, Paterson AM (2008) Evolution of New Zealand’s terrestrial fauna: a review of molecular evidence. Phil Trans R Soc B 363:3319–3334
- Graham DH (1953) A treasury of New Zealand fishes. Reed, Wellington, N Z, 404 pp
- Grandcolas P, Muriene J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: a very old Darwinian island. Phil Trans R Soc B 363:3309–3317

- Günther A (1866) Catalogue of the fishes in the British Museum, vol 8. British Museum, London
- Günther A (1870) Notes on *Prototroctes*, a fish from fresh waters of the Australian region. Proc Zool Soc London 1870:150–152
- Haddrath O, Baker AJ (2001) Complete mitochondrial DNA genome sequence of extinct birds: ratite phylogenetics and vicariance biogeography hypothesis. Proc R Soc Lond B Biol Sci 268:939–945
- Hale R, Swearer SE (2008) Otolith microstructure and microchemical changes associated with settlement in the diadromous fish *Galaxias maculatus*. Mar Ecol Prog Ser 354:229–234
- Hale R, Downes BJ, Swearer SE (2008) Habitat selection as a source of interspecific recruitment of two diadromous fish species. Freshwater Biol 53:2145–2157
- Harshmann J, Braun EL, Braun MJ, Huddleston CJ, Bowie RCK, Chojnowski JL, Hackett SJ, Han K-L, Kimball RT, Marks BD, Miglia KJ, Moore WS, Reddy S, Sheldon FH, Steadman DW, Steppan SJ, Witt CC, Yuri T (2008) Phylogenomic evidence for multiple losses of flight in ratite birds. Proc Natl Acad Sci 105:13462–13467
- Hector J (1872) Notes on the edible fishes. In: Hutton FW, Hector J (eds) Fishes of New Zealand. Hughes, Wellington, N Z, pp 97–133
- Hector J (1903) Notes on the New Zealand whitebait. Trans Proc N Z Inst 35:312–319
- Hefford AE (1931a) Whitebait. N Z Mar Dep Ann Rep Fish 1930:21–23
- Hefford AE (1931b) Whitebait. N Z Mar Dep Ann Rep Fish 1931(14):16–17
- Hefford AE (1932) Whitebait investigation. N Z Mar Dep Ann Rep Fish 1932:13–15
- Hennig W (1966) Phylogenetic systematic. University of Illinois, Urbana, IL, 263 pp
- Hickford MJH, Schiel DR (2003) Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Mar Ecol Prog Ser 252:255–271
- Hill RS (2001) Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record. Aust J Bot 49:321–332
- Humphries CJ, Parenti LR (1999) Cladistic biogeography: interpreting patterns of animal and plant distributions, 2nd edn. Oxford University Press, Oxford, 187 pp
- Hutton FW (1872) Catalogue, with diagnoses of the species. In: Hutton FW, Hector J (eds) Fishes of New Zealand. Hughes, Wellington, New Zealand, pp 1–93
- Hutton FW (1873) On the geographical relations of the New Zealand fauna. Trans Proc N Z Inst 5:227–256
- Hutton FW (1884) On the origin of the fauna and flora of New Zealand. N Z J Sci 2:1–20
- Hutton FW (1901) On a marine *Galaxias* from the Auckland Islands. Trans Proc N Z Inst 34:198–199
- Ishiguro NB, Miya M, Nishida M (2003) Basal euteleostean relationships: a mitogenomic perspective on the phylogenetic reality of the Protacanthopterygii. Mol Phyl Evol 27:476–488
- Jenyns L (1842) Fish. In: Darwin C (ed) The zoology of the voyage of HMS Beagle, vol 4. Smith Elder, London, pp 1–172
- Johnson GD, Patterson C (1996) Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic, New York, pp 251–332
- Johnston RM (1883) General and critical observations on the fishes of Tasmania, with a classified catalogue of all the known species. Pap Proc R Soc Tasm 1882:53–144
- Keast RA (1968) Evolution of mammals on southern continents: I. Introduction: the southern continents as backgrounds for mammalian evolution. Quart Rev Biol 43:225–233
- Keast RA (1971) Continental drift and the evolution of the biota on southern continents. Quart Rev Biol 46:335–378
- Knapp M, Stockler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ (2005) Relaxed molecular clock provides evidence for long-distance dispersal by *Nothofagus* (southern beech). PLoS Biol 3:38–43
- Kodandaramaiah U (2009) Vagility: the neglected component in historical biogeography. Evol Biol 36:327–355

- Lagler KF, Bardach JE, Miller RR (1962) Ichthyology: the study of fishes. Wiley, New York, 506 pp
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Lomolino MV, Riddle BR, Brown JH (2006) Biogeography. Sinauer, Sunderland, MA, 447 pp
- Macleay W (1883) On a species of *Galaxias* found in the Australian Alps. *Proc Linn Soc NSW* 7:106–109
- Manter HW (1955) Parasitological reviews: the zoogeography of trematodes of marine fishes. *Exper Parasit* 4:62–86
- Mardones A, Vega R, Encina F (2008) Cultivation of whitebait (*Galaxias maculatus*) in Chile. *Aquac Res* 39:731–737
- McCulloch AR (1915) The migration of the jollytail, or eel-gudgeon, *Galaxias attenuatus*, from the sea to fresh-water. *Aust Zool* 1:47–49
- McDowall RM (1964a) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1964b) A consideration of the question: “What is whitebait?”. *Tuatara* 12:134–146
- McDowall RM (1966) Further observations on *Galaxias* whitebait and their relation to the distribution of the Galaxiidae. *Tuatara* 14:12–18
- McDowall RM (1968a) *Galaxias maculatus* (Jenyns) – the New Zealand whitebait. *N Z Mar Dep Fish Res Bull* 2:1–84
- McDowall RM (1968b) The application of the terms anadromous and catadromous to the Southern Hemisphere salmonoid fishes. *Copeia* 1968:176–178
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970a) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool, Harv Univ* 139:341–431
- McDowall RM (1970b) A second species of *Galaxias* common to Tasmania and New Zealand (Pisces: Galaxiidae). *Rec Dom Mus, Wellington* 7:13–19
- McDowall RM (1971) Fishes of the family Aplochitonidae. *J R Soc N Z* 1:31–52
- McDowall RM (1972) The species problem in freshwater fishes, and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *J R Soc N Z* 2:325–367
- McDowall RM (1973) Zoogeography and taxonomy. *Tuatara* 20:88–96
- McDowall RM (1975) A revision of the New Zealand species of *Gobiomorphus* (Pisces; Eleotridae). *Nat Mus N Z Rec* 1:1–32
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1984) The New Zealand whitebait book. Reed, Wellington, N Z, 210 pp
- McDowall RM (1988) Diadromy in fishes: migrations between marine and freshwater environments. Croom Helm, London, 309 pp
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (2001) How many species of *Galaxias* are there in Africa? *Ichthos* 67:10–11
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *Environ Biol Fish* 29:207–220
- McDowall RM (2005) Biogeography of the Falkland Islands: converging trajectories in the South Atlantic. *J Biogeogr* 32:49–62
- McDowall RM (in press) Ikawai: freshwater fishes in Maori culture and economy. Canterbury University Press, Christchurch, N Z
- McDowall RM, Eldon GA (1980) The ecology of whitebait migrations (Galaxiidae: *Galaxias* spp.). *N Z Min Agric Fish. Fish Res Bull* 20:1–171
- McDowall RM, Fulton W (1996) Family Galaxiidae – galaxiids. In: McDowall RM (ed) Freshwater fishes of south-eastern Australia. Reed, Chatswood, NSW, pp 52–77

- McDowall RM, Kelly GR (1999) Date and age at migration in juvenile giant kokopu, *Galaxias argenteus* (Gmelin) (Teleostei: Galaxiidae) and estimation of spawning season. *N Z J Mar Freshwater Res* 33:263–270
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. *N Z J Zool* 29:41–52
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. *J R Soc N Z* 33:675–691
- McDowall RM, Mitchell CP, Brothers EB (1994) Age at migration from the sea of juvenile *Galaxias* in New Zealand. *Bull Mar Sci* 54:385–402
- McDowall RM, Robertson DA, Saito R (1975) Occurrence of galaxiid larvae and juveniles in the sea. *N Z J Mar Freshwater Res* 9:1–9
- McKenzie DH (1904) Whitebait at the antipodes. *N Z Illustr Mag* 10:122–126
- McLean JL (1974) Anadromous whitebait. *Aust Fish* 33:33
- McLoughlin S (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Am J Bot* 49:271–300
- Meek A (1916) The migrations of fish. Arnold, London, 437 pp
- Myers GS (1938) Freshwater fishes and West Indian zoogeography. *Smithson Rep* 1937:339–364
- Myers GS (1949) Salt tolerance of fresh-water fish groups in relation to zoogeographical problems. *Bijdr Dierk* 28:315–322
- Myers GS (1951) Freshwater fishes and East Indian zoogeography. *Stanf Ichthyol Bull* 4:11–21
- Myers GS (1953) Palaeogeographic significance of fresh-water fish distribution in the Pacific. *Proc 7th Pac Sci Congr* 4:38–49
- Nelson GJ (1969) The problem of historical biogeography. *Syst Zool* 18:243–246
- Nelson GJ, Ladiges PY (2001) Gondwana, vicariance and the New York school revisited. *Aust J Bot* 49:389–409
- Phillipps WJ (1919) Life history of the fish *Galaxias attenuatus*. *Aust Zool* 1:211–213
- Phillipps WJ (1926) Origins of the freshwater fishes of New Zealand. *Nature* 117:485–486
- Pollard DA (1971) The biology of a landlocked form of the normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns): life cycle and origin. *Aust J Mar Freshwater Res* 22:91–123
- Popper KR (1968) The logic of scientific discovery. Hutchinson, London, UK (revd. edn.), 480 pp
- Powell L (1870) On four fishes commonly found in the River Avon, with a consideration of the question: “What is whitebait?”. *Trans Proc N Z Inst* 2:84–87
- Raadik T (2008) Family Galaxiidae: galaxiids, mudfishes and whitebaits. In: Gomon M, Bray D, Kuiter R (eds) *Fishes of Australia’s south coast*. Reed New Holland, Sydney, NSW, pp 217–222
- Regan CR (1905) A revision of the fishes of the family Galaxiidae. *Proc R Soc Lond* 2:363–384
- Regan CT (1913) The Antarctic fishes of the Scottish National Antarctic expedition. *Trans R Soc Edinb* 49:229–292
- Reid RC (1886) *Rambles on the Golden Coast of the South Island of New Zealand*. Colonial Printing and Publishing Company, London, 176 pp
- Rosen DE, Croizat L, Nelson GJ (1974) Centers of origin and related concepts. *Syst Zool* 23:265–287
- Rosen DE (1974a) Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. *Bull Am Mus Nat Hist* 153:265–326
- Rosen DE (1974b) Space, time form: the biogeographical synthesis, by Leon Croizat (review). *Syst Zool* 23:288–290
- Rosen DW (1978) Vicariant patterns and historical explanation in biogeography. *Syst Zool* 24:431–464
- Rowe DK, Kelly GR (2009) Duration of the oceanic phase for inanga whitebait (Galaxiidae) is inversely related to growth rate at sea. *Amer Fish Soc Symp* 69:343–354
- Ruttenberg BI, Hamilton SL, Hickford MJH, Paradis GL, Sheehy MS, Standish JD, Ben-Tzvi O, Warner RR (2005) Elevated levels of trace elements in the cores of otoliths and their potential use as natural tags. *Mar Ecol Prog Ser* 297:273–281

- Scott TD, Glover CJM, Southcott RV (1974) The marine and freshwater fishes of South Australia. Government Printer, Adelaide, SA, 392 pp
- Simpson GG (1940) Antarctica as a faunal migration route. *Proc 6th Pac Sci Congr* 2:755–768
- Simpson GG (1952) The probabilities of dispersal in geological time. *Bull Am Mus Nat Hist* 99:163–176
- Smith GW (1909) A naturalist in Tasmania. Oxford University Press, Oxford, 151 pp
- Stokell G (1945) The systematic arrangement of the New Zealand Galaxiidae. Part I. Generic and sub-generic classification. *Trans R Soc N Z* 75:124–137
- Stokell G (1950) Freshwater fishes from the Auckland and Campbell Islands. *Cape Exped Ser Bull N Z Dep Sci Ind Res* 9:1–8
- Stokell G (1953) The distribution of the family Galaxiidae. *Proc 7th Pac Sci Congr* 4:48–52
- Stokell G (1955) Freshwater fishes of New Zealand. Simpson & Williams, Christchurch, N Z, 145 pp
- Stokell G (1966) A preliminary investigation of the systematics of some Tasmanian Galaxiidae. *Pap Proc R Soc Tasm* 100:73–79
- Swenson U, Backlund A, McLoughlin S, Hill RS (2001) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* 17:28–47
- Waite ER (1909) Vertebrata of the sub-Antarctic islands of New Zealand. In: Chilton C (ed) the sub-Antarctic islands of New Zealand. Philosophical Institute of New Zealand, Christchurch N Z, pp 542–600
- Wallace AR (1876) The geographical distribution of animals. McMillan, London, 2 vols
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Waters JM, BurrIDGE CP (1999) Extreme intraspecific mitochondrial DNA sequence divergence in *Galaxias maculatus* (Osteichthyes: Galaxiidae), one of the world's most widespread freshwater fish. *Mol Phyl Evol* 11:1–12
- Waters JM, Cambray JA (1997) Intraspecific phylogeography of Cape galaxias from South Africa: evidence from mitochondrial DNA sequence. *J Fish Biol* 50:1329–1338
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, White RWG (1997) Molecular phylogeny and biogeography of the Tasmanian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Aust J Zool* 45:39–48
- Waters JM, Dijkstra LH, Wallis GP (2000a) Biogeography of a Southern Hemisphere freshwater fish: how important is marine dispersal? *Mol Ecol* 9:1815–1821
- Waters JM, Lopez JA, Wallis GP (2000b) Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthys: Galaxiidae): dispersal, vicariance and the place of *Lepidogalaxias salamandroides*. *Syst Biol* 49:777–795
- Whitley GP (1935) Whitebait. *Vict Nat* 52:41–51
- Whitley GP (1956) New fishes from Australia and New Zealand. *Proc R Zool Soc N S W* 1945–55:34–38
- Wiley EO (1987) Methods in vicariance biogeography. In: Systematics and evolution: a matter of diversity. Utrecht University, Utrecht, The Netherlands, pp 283–306
- Wiley (1988) Vicariance biogeography. *Ann Rev Syst Ecol* 19:513–542

Chapter 9

Broad-Scale, Macroecological Patterns, Ranges and Community Species Richness in the Fauna

Abstract Macroecological patterns in the New Zealand freshwater fish fauna are structured largely around the presence and absence of diadromy. All diadromous species are present across nearly the entire latitudinal range of New Zealand, and they exhibit general sympatry with other diadromous species, whereas non-diadromous species have much narrower latitudinal ranges, the species composition of communities changes progressively from northern to southern latitudes, and there is widespread allopatry. Inland penetration of diadromous species varies widely with some restricted to lowland habitats close to the sea, whereas other species penetrate varying distances inland. As a result there is downstream-upstream decline in species richness of diadromous fish communities, as one species after another drops out of the communities, with increasing distance inland/elevation, a form of nestedness. Species richness at any latitude is dominated by diadromous species. Non-diadromous species vary widely in their centres of occupation, though many of them are most commonly found at sites well upstream from the sea. Non-diadromous species are largely absent from small islands around New Zealand, probably because island streams are small and ephemeral.

Keywords Diadromy • Galaxiidae • Geographic range • Inland penetration • Macroecology • Species richness

9.1 General Patterns of Distribution: Diadromy and Latitudinal Range

The latitudinal ranges of the various species (or lineages of species) in the New Zealand freshwater fish fauna, listed in [Table 1.1](#), are plotted in [Fig. 9.1](#), which illustrates presence/absence of extant species in the fauna at the New Zealand-wide scale. To compile this figure, the presence of each fish species in half-degree wide latitudinal bands across the country is indicated (see [Fig. 6.2](#)). Diadromous species are grouped in the upper panel of [Fig. 9.1](#), whereas non-diadromous species are

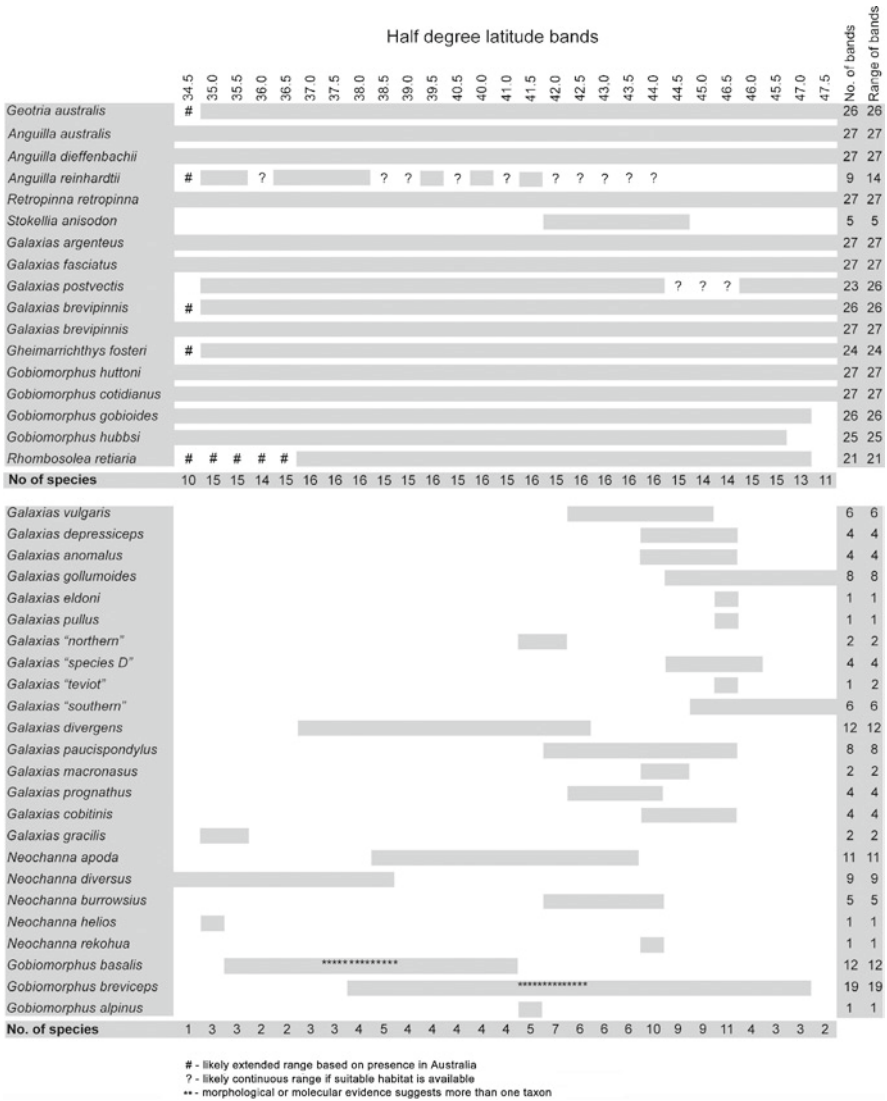


Fig. 9.1 Distributions of diadromous (upper panel) and non-diadromous (lower panel) freshwater fish species across the length of New Zealand, based on their presence in the half-degree latitudinal bands across the country shown in Fig. 6.2. (?? indicate absences within the broader latitudinal ranges of diadromous species, probably indicating sampling deficiencies or lack of suitable proximal habitats; # indicate these species present in Australia, further north than they are present in New Zealand)

grouped in the lower panel. Two columns of numbers down the right margin of Fig. 9.1 comprise:

- (i) The latitudinal range (number of bands) across which each species is recorded, from north to south

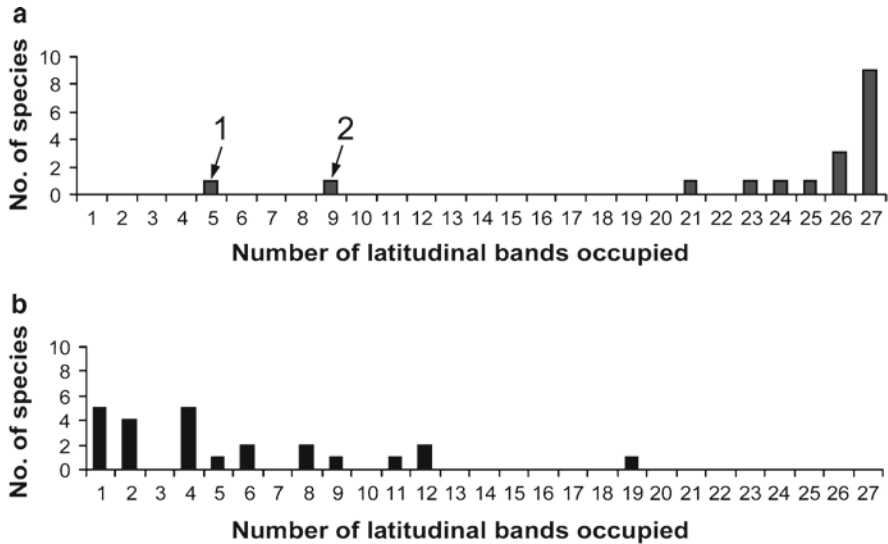


Fig. 9.2 Number of half-degree latitudinal bands shown as ordered by increasing number of bands in which a. diadromous and b. non-diadromous species are found: note the strong dichotomy, with diadromous species far more widely present. **Arrows** – ↑1: number of sites for Stokell's smelt, *Stokellia anisodon*; ↑2 – sites for spotted eel, *Anguilla reinhardtii*, two diadromous species with unusually narrow ranges

(ii) The number of half-latitude bands *within which each species is present* (these are further plotted in Fig. 9.2)

These two rows of numbers for any species will differ only when that species is absent from latitudinal bands within its overall latitudinal range – as is true in a few instances (e.g., spotted eel, shortjaw kokopu – Fig. 9.1). Two horizontal rows of numerals, one across the middle of the figure (below the upper panel) and the other at the bottom of the figure (below the lower panel), indicate the number of species recorded (species richness) in each half-degree latitudinal band for diadromous and non-diadromous species, respectively.

It is immediately clear from perusal of Fig. 9.1, that most of the diadromous species are present in nearly all of the half-degree latitudinal bands, and so are recorded along virtually the entire latitudinal range of New Zealand (from north to south), as shown by the presence in 14 of the 17 diadromous species in 21 or more of the 27 latitudinal bands (Fig. 9.2a). Occasional gaps for species within their broad latitudinal ranges (signified by '?' in Fig. 9.1) may reflect collection inadequacies rather than absences of species from some latitudinal bands, though it could also be due to the lack of suitable habitats in that band. Many species are recorded also from Stewart Island, in the far south (though there are, as yet, relatively few sampling sites there – only 52 – and we still may not know the island's fauna at all well). Similarly, absences of some species at the northern limits of their latitudinal ranges in New Zealand (signified by # in Fig. 9.1) may also reflect lack of sampling, rather than indicating habitat suitability/temperature latitudinal limitations,

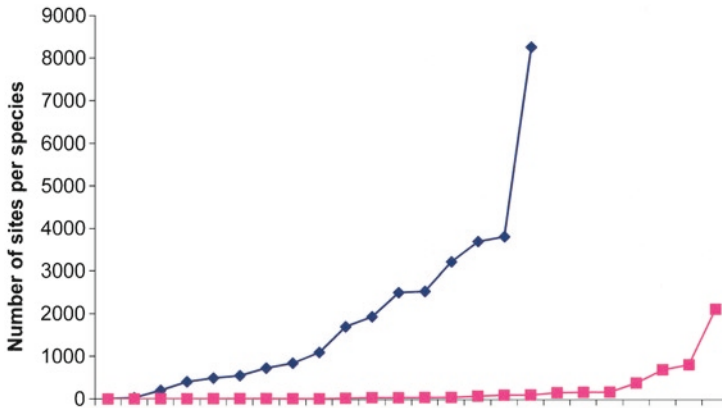


Fig. 9.3 Broad variation in the number of NZFFD sites at which: Diadromous species – blue line; nondiadromous species – red line, the species ordered, in each instance, as an increasing numbers of sites

as some such species are present at lower latitudes in eastern Australia than they are in New Zealand. These details aside, the key point is that the diadromous species are typically present nearly continuously along the length of New Zealand, with occasional absences, some of them possibly owing primarily to absence of suitable habitats.

The number of sites throughout New Zealand from which each species has been recorded is plotted for diadromous and non-diadromous species in Fig. 9.3. Diadromous species are usually known from more than 5,000 sites per species, which is consistently much higher than for non-diadromous species, most of which are known from less than 500 sites. Thus, the broad latitudinal ranges of diadromous species (Figs. 9.1 and 9.2) are consistent with these species tending to be recorded from many more localities than non-diadromous ones, though there is rather broader overlap between diadromous and non-diadromous species in the total number of site records, than there is overlap in their latitudinal ranges (Figs. 9.1 and 9.2). This broader overlap is, in part, because some diadromous species, despite being latitudinally widespread (Fig. 9.1), are relatively rare within their broad latitudinal ranges (e.g. shortjaw kokopu, giant bully), whereas some non-diadromous species, though having relatively narrower latitudinal ranges (Fig. 9.1), are represented at many sites within those more restricted latitudinal ranges as is true in upland bully, Cran's bully and Canterbury galaxias.

Significant exceptions to the generalisation that diadromous species are virtually New Zealand-wide in range (as indicated by their presence in most half degree latitudinal bands) are:

- (i) Stokell's smelt (Fig. 9.2a, arrow 1) – which is known from very few sites across a very limited extent of the east coast of the central South Island (and see Fig. 10.1).

- (ii) The eastern Australian spotted eel (Fig. 9.2a, arrow 2) – which has, so far, been found at relatively few sites, is primarily northern in range, and may still be invading New Zealand river systems more widely, though we know nothing about the processes involved in its arrival and establishment.

9.2 Latitudinal Variation in the Frequency of Occurrence of Diadromous Species

Some species appear to be more sparsely present at the northern or southern extremities of their ranges. Visual inspection of distribution maps shows that koaro, for instance, is widely present to the south but is far less often found in the far north (Fig. 9.4d); the same is true of lamprey (Fig. 9.4a) and black flounder (Fig. 9.4f).

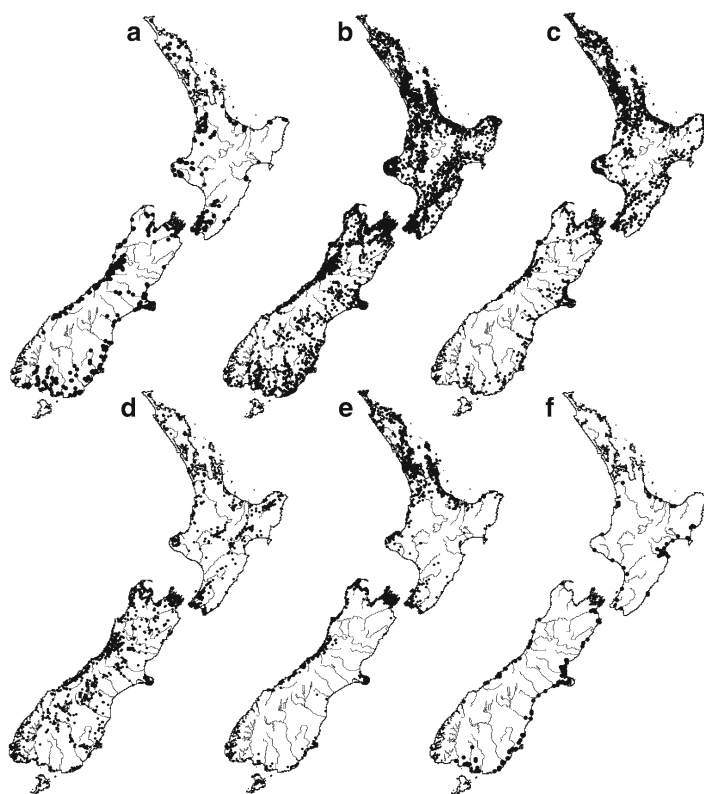


Fig. 9.4 Distributions of a variety of diadromous species across New Zealand, with widely varying inland penetration: some species, such as: b: longfin eel, *Anguilla dieffenbachii* (family Anguillidae), and d: koaro, *Galaxias brevipinnis* penetrating long distances inland, whereas others, such as f: black flounder are restricted to low elevations, close to the coast; Distributions of: a: lamprey, *Geotria australis*; b: longfin eel, *Anguilla dieffenbachii*; c: shortfin eel, *A. australis*; d: koaro, *Galaxias brevipinnis*; e: banded kokopu, *Gl. fasciatus*; f: black flounder, *Rhombosolea retiaria*

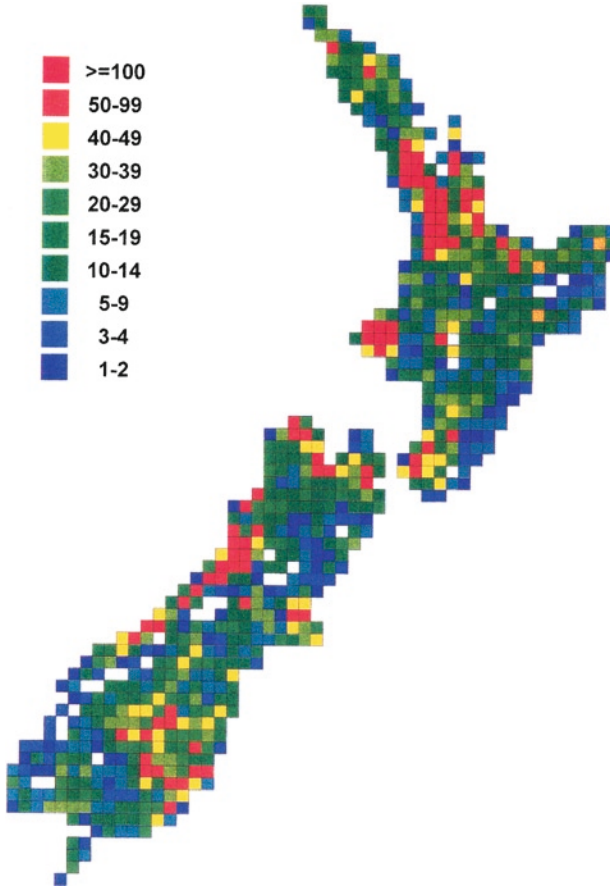


Fig. 9.5 Regional concentrations of sampling locations across the New Zealand landscape based on 10km grid squares

In contrast, shortfin eel and banded kokopu are widespread at northern latitudes but appear sparser in the south (Fig. 9.4c, e).

These patterns of latitudinal occurrence were further explored by plotting the frequency distributions of species' records across the length of New Zealand. This was done by dividing the country into 30 bands based on the national New Zealand Mapping Series 260 topographical maps, using map coordinates for sites in the New Zealand Freshwater Fish Database (NZFFD). Because the intensity of sampling represented in the NZFFD varies widely across the New Zealand landscape (Fig 9.5) the number of each species' records within each of these bands depends, in part, on sample site frequency within each band. Frequencies were therefore standardized against the band with the highest number of recorded sites (Table 9.1). The standardised frequencies were then plotted along the length of the country and the results of this plot demonstrate that, as noted above, there is in some species a

significant north/south change in intensity of occurrence: in some their occurrence increases with increasing latitude (lamprey – Fig. 9.6a; koaro – Fig. 9.6d; and also in black flounder), whereas in others occurrence decreases with latitude (shortfin eel – Fig. 9.6b and banded kokopu – Fig. 9.6c), so that these species tend to be more northern in presence. Interestingly, data for species composition in the commercial New Zealand’s freshwater eel fishery, show a parallel shift in the proportional composition of the commercial eel fishery by species, with shortfins predominating at northern latitudes and longfins at southern ones (McDowall 1990).

There are several other points here of biogeographic interest. There are instances where New Zealand species that are present also in Australia, sometimes exhibit a tendency for more frequent presence in northern New Zealand, e.g. shortfin eel (Fig. 9.6b). However, both lamprey or koaro are both present in eastern Australia and Tasmania, too, and so well north of their latitudinal range in New Zealand though they are two species that have a stronger presence in southern rather than northern New Zealand. These two species also display other, more southern, linkages, e.g., the lamprey is found in Patagonian South America, and the koaro is the only freshwater fish present on the Auckland and Campbell Islands far to the south of New Zealand. Perhaps, however, the most interesting aspect of all of these distributions is that they show that, while diadromous species are mostly present widely from north to south across New Zealand latitudes (Fig. 9.1), there is nevertheless distinctive pattern within these widespread distributions for each species, i.e., they are sometimes not evenly widespread along the length of New Zealand. Ecological studies, such as exploration of temperature tolerances or preferences of each species are needed to clarify and explain these differences.

9.3 Distinctive Distribution Patterns of the Landlocked Populations of Normally Diadromous Species

Six diadromous species in the New Zealand fauna can establish landlocked populations: viz. common smelt, koaro, inanga, giant kokopu, banded kokopu, and common bully. Their patterns of occurrence in the lake populations across ranges of elevation and penetration probably just reflect the patterns of availability, accessibility, and habitat suitability of the lakes, themselves. In some instances the elevation/inland penetration profiles for lakes sites of these species are similar for diadromous and lacustrine populations, but in others the elevations/distances inland of the lakes occupied by landlocked populations of diadromous species substantially exceed the elevations/distances inland where diadromous populations of these species are found (Table 9.1; see Fig. 5.6). This seemingly indicates that at some past time[s], these species have managed to penetrate further inland to reach the various inland lakes than is revealed by contemporary surveys of diadromous populations in the same river/lake catchments. Landlocked populations of some species are found in landlocked lakes that are now inaccessible to immigrants of otherwise diadromous species penetrating river systems from downstream. Some of these implicate koaro populations in some high elevation montane or submontane tarns, and how the fish originally reached some of these lakes

Table 9.1 Standardised data on records of diadromous species’ presence in latitudinal strata, north to across New Zealand (data are standardised against the number of records in the most-sampled stratum)

Standardised number of sites per species per stratum										
Stratum number	No. of sites in stratum	Ratio to largest number of sites – stratum 21	<i>Georria australis</i>	<i>Anguilla australis</i>	<i>Anguilla dieffenbachii</i>	<i>Retropinna retropinna</i>	<i>Stokellia anisodon</i>	<i>Galaxias argenteus</i>	<i>Galaxias fasciatus</i>	<i>Galaxias postvectis</i>
1	506	3.0	6	428	328	182	0	0	391	15
2	362	4.2	30	420	594	165	0	0	314	17
3	185	8.3	0	415	514	33	0	0	622	25
4	589	2.6	5	391	628	36	0	31	652	3
5	1,371	1.1	2	569	642	84	0	13	621	4
6	859	1.8	13	540	661	273	0	39	175	4
7	1,165	1.3	38	630	823	246	0	87	237	38
8	912	1.7	29	263	621	153	0	19	89	29
9	601	2.6	3	209	608	79	0	13	36	13
10	1,535	1.0	20	207	884	47	0	25	89	84
11	638	2.4	58	286	746	166	0	31	22	17
12	272	5.6	0	367	931	181	0	11	40	0
13	472	3.3	33	312	907	78	0	39	289	169
14	963	1.6	67	268	810	53	0	104	289	148
15	997	1.5	48	302	807	38	0	68	169	63
16	136	11.3	34	214	700	0	0	23	181	45
17	585	2.6	18	189	601	5	0	58	108	63
18	919	1.7	90	104	795	8	0	38	50	50
19	1,079	1.4	44	193	603	20	3	239	245	166
20	698	2.2	46	389	526	62	18	53	125	20
21	1,233	1.2	75	251	513	71	9	81	136	22
22	562	2.8	46	74	344	46	11	137	93	5
23	466	3.3	7	53	224	23	0	13	20	0
24	731	2.1	36	46	197	50	17	2	0	0
25	766	2.0	20	56	299	22	0	12	22	0
26	468	3.3	49	56	538	10	0	20	128	0
27	524	2.9	64	67	560	41	0	53	111	0
28	122	12.6	113	151	805	38	0	75	88	0
29	443	2.5	107	225	717	104	0	163	142	17
30	116	13.2	66	145	475	119	0	238	264	0
20,275			Regression equation	$y = 2.28x + 3.57$	$y = 12.40x + 365.66$	$y = -5.66x + 701.1$	$y = -3.9152x + 141.79$	$y = 3.47x + 2.32$	$y = -11.25x + 365.91$	$y = -0.63x + 43.68$
R			0.4190	0.4173	0.0641	0.2248	0.2304	0.3068	0.0131	
			$p < 0.001$	$p < 0.001$	$0.5 > p > 0.2$	$0.01 > p > 0.001$	$0.01 > p > 0.001$	$0.01 > p > 0.001$	$p > 0.1$	

(continued)

Table 9.1 (continued)

<i>Galaxias brevipinnis</i>	<i>Galaxias maculatus</i>	<i>Cheimarrichthys fosteri</i>	<i>Gobionomorphus huttoni</i>	<i>Gobionomorphus cotidianus</i>	<i>Gobionomorphus gobioides</i>	<i>Gobionomorphus hubbsi</i>	<i>Rhombosolea retziaria</i>	Number of species per stratum			
								Min	Max	Mean	Median
27	282	112	373	300	127	18	0	0	7	1.72	1
64	263	174	246	250	81	17	0	0	7	1.94	2
8	340	58	423	415	100	33	0	0	7	2.09	2
10	399	73	430	433	112	13	0	0	8	1.94	2
38	224	100	273	352	43	3	0	0	10	1.80	2
30	232	200	132	456	5	0	2	0	9	2.28	1
70	252	252	290	410	49	70	5	0	9	1.41	1
106	91	145	177	374	8	59	7	0	8	1.20	0
125	151	69	235	268	3	26	8	0	12	1.44	1
156	102	96	271	196	10	22	4	0	9	1.59	1
36	149	255	284	265	29	65	31	0	6	1.54	1
23	147	175	119	339	17	11	6	0	8	2.08	2
130	345	111	394	299	62	33	7	0	12	2.16	2
328	266	99	547	179	59	91	6	0	8	1.79	1
182	269	111	311	273	26	71	9	0	6	1.21	1
293	68	45	147	90	11	11	0	0	9	1.32	1
157	147	126	205	129	8	81	10	0	8	1.64	1
187	130	220	381	215	13	220	12	0	9	2.00	1
358	221	145	347	327	3	154	3	0	10	1.84	1
222	185	277	90	429	44	218	123	0	9	1.72	1
249	289	203	181	309	51	154	42	0	8	1.20	0
287	93	117	139	314	11	101	14	0	8	0.69	0
201	82	20	33	349	3	23	13	0	9	0.59	0
101	23	44	19	271	4	52	42	0	6	0.54	0
134	46	4	28	160	8	8	10	0	9	0.88	1
167	112	10	102	105	36	20	7	0	6	1.05	1
152	164	53	105	217	0	0	26	0	6	1.29	1
113	138	25	189	201	0	0	38	0	8	1.67	1
139	249	80	270	402	17	62	94	0	5	1.56	2
198	356	0	304	158	13	0	53	0	7	0.89	0
y = -5.90	y = -4.02	y = -3.50	y = -6.82	y = -4.76	y = -2.42	y = 1.09	y = -01 =	y = -0.03			
+ 51.51	+	+	+	+	+	+	26.38	+			
	256.21	167.60	340.54	n356.63	69.21	37.70		1.99			
0.2933	0.1272	0.1565	0.2069	0.1688	0.3706	0.0244	0.0196	0.3401			
0.01 > p >	0.1 > p >	0.5 > p >	0.01 > p >	0.5 > p >	p < 0.001	p > 0.1	p < 0.001				
0.001	0.05	0.2	0.001	0.02							

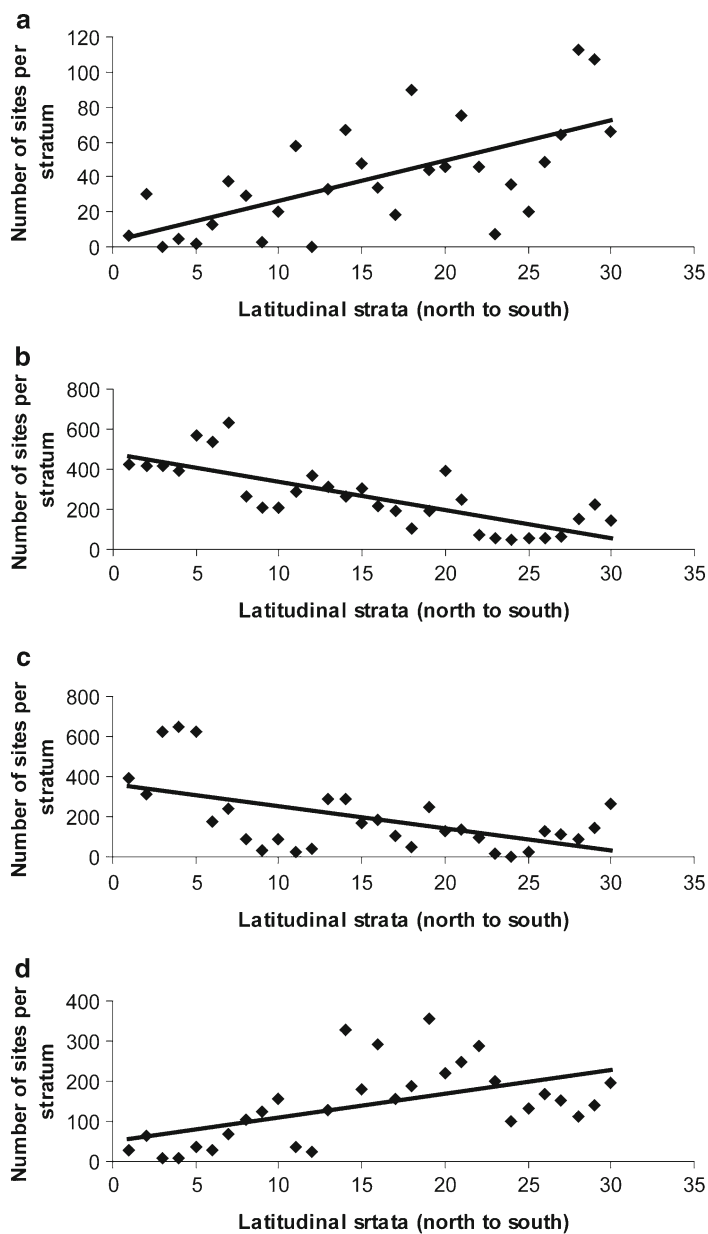


Fig. 9.6 Latitudinal changes in standardised occurrence of diadromous species: **a.** lamprey, *Geotria australis*; **b.** shortfin eel, *Anguilla australis*; **c.** banded kokopu, *Galaxias fasciatus*; **d.** koaro, *Gl. brevipinnis*

sometimes defies the imagination. Presumably there were once fluvial connections to these lakes that facilitated their occupation by koaro, though this would seem to be unlikely under the present configurations of the lakes – some of them have no semblance of an outflowing stream. So present distributions of some of these lake populations are indicative of former lake/stream configurations that have disappeared, perhaps because of tectonic changes.

9.4 Narrower Ranges of Non-diadromous Species

Non-diadromous species tend to have much more limited latitudinal ranges along the length of New Zealand (the lower panel in Fig. 9.1) than diadromous species; also they tend to be present in far fewer half-degree latitudinal bands (Fig 9.1 – compare the upper and lower panels; and see Fig. 9.2b). Some non-diadromous species are present across only very narrow latitudinal ranges (dune lakes galaxias, black, burgundy, and Canterbury mudfishes, lowland longjaw galaxias, bignose galaxias, Teviot galaxias, Tarndale bully, and others). However, a few non-diadromous species, such as dwarf galaxias, upland and Cran’s bully, have distinctively wider latitudinal ranges. Non-diadromous species tend, in general, also to be represented at far fewer NZFFD sites (Table 9.1; Fig. 9.2b). As well, apparently broad latitudinal ranges of upland and Cran’s bullies may, in part, reflect the fact that more than one distinct species is ‘captured’ in each of these names – current taxonomy may not reflect actual species diversity (e.g. Smith et al. 2005 and Stevens and Hicks, 2009, in upland bully).

In most instances non-diadromous species are limited to either, and only, the North or South Islands of New Zealand, though there are several exceptions. Upland bully (see also Fig. 15.2 – blue symbols, and discussion of the detailed ranges of this species) is known widely in the southern North Island, throughout the northern and eastern South Island and on Stewart Island in the far south. Dwarf galaxias and brown mudfish are widely present in the southern North Island and the northwestern South Island, but are absent from the eastern South Island (see Figs 12.2, blue symbols, and Fig. 14.3, brown symbols). In the absence of these two latter species in the eastern South Island, there is replacement by likely sister species, specifically alpine galaxias (Fig. 12.2 – green symbols) and Canterbury mudfish (Fig. 14.3 – red symbols).

9.5 Presence of Freshwater Fishes on the Islands Around New Zealand

There are many, mostly small, nearshore islands around the New Zealand coastline, usually within about 50 km of the three ‘mainland’ islands (North, South and Stewart). Most of these nearshore islands are small, but some have permanently (or

perhaps semi-permanently) flowing streams in which fish may be found. Table 9.2 lists the small islands from which freshwater fish are known and the species that are present. In all but one instance, species known from these islands are diadromous.

The exception is that dwarf galaxias is present on D'Urville Island (see Fig. 12.2, arrow 4). This island is among the larger ones (third largest of the smaller, near-shore islands with area of 150 km²), and is also the island closest to the mainland (<1 km); it would probably have had land/fluviial connections with the South Island, only a few thousand years ago when sea levels were as much as 135 m lower and coastlines were substantially extended seawards (Kirk 1994; Pillans et al. 1992). D'Urville Island's mainland connections may also have been more recent than those of other more distant islands simply as a consequence of its close proximity to the northern South Island and the shallowness of the seas separating it.

Though detailed surveys of some of the islands are yet to be undertaken, the larger islands (e.g., Great Barrier, the largest of these at 285 sq. km) have the most speciose faunas (Table 9.2).

Some diadromous species are found on none of these islands (lamprey, common smelt, torrentfish), and some are only rarely found there (shortjaw kokopu, giant kokopu, common bully, bluegill bully). Given the generally widespread ranges of these diadromous species on the mainland islands of New Zealand, their absences from the smaller islands are probably due to the smaller islands having smaller stream catchments, leading to streams being ephemeral, though there may also be issues of recruitment to these small islands (little is known). Many of the islands are now deforested, and this may have led to a loss of fish species from the small streams on islands, probably both because some species appear to prefer streams with riparian forest (koaro, banded kokopu), and perhaps also because removal of riparian forest may have made stream flows more 'flashy' with shorter, higher peak flood flows and longer-lasting low flows between flood events.

New Zealand also several largish, more distant, islands, such as Chatham (900 sq. km and c. 800 km to the east of mainland New Zealand), the Auckland Islands (510 sq. km and 300 km away to the south) and Campbell Island (115 sq. km and 590 km southeast), where freshwater fish are present.

Ten freshwater fish species are known on the Chatham Islands (Table 9.2; Young 1929; Skrzynski 1967; Rutledge 1992, NZFFD data). Only one of these, the Chatham mudfish, is non-diadromous, and it is the only species endemic to Chatham Island (McDowall 2004). Issues relating to its phylogenetic relationships and biogeography are discussed elsewhere – see Chapter 14).

9.6 Freshwater Fishes on the Chatham Islands

In the light of the diadromous species that are *present* at the Chathams, there are some perhaps surprising *absences*, such as shortjaw kokopu, common bully, bluegill bully, and torrentfish, all of which are widespread on the main islands. For all

the diadromous species, recruitment of progeny back to these very isolated islands may be a problem, and the behavioural and oceanographic mechanisms that enable diadromous species to recruit to the Chathams are unknown. The effects of ocean currents, and their impact on the recruitment of juveniles into Chatham Island river systems from the sea, may be critical elements in determining the freshwater fishes present there. It is not known whether the freshwater fish populations of these islands self-recruit, or actually derive their recruits from mainland New Zealand, and perhaps there is some of both. Oceanographer Stephen Chiswell (NIWA, Wellington, N Z, 2007, personal communication), from models of surface ocean currents in the seas between New Zealand and the Chatham Islands, has suggested that, even after 180 days at sea (about the duration of life at sea in inanga – McDowall et al. 1994), regular, passive, cohort-scale recruitment of oceanic larval progeny of freshwater fish species from mainland New Zealand to the Chatham Islands is unlikely. Thus the derivations of diadromous progeny of freshwater fish from New Zealand to the Chathams probably needs to be addressed as occasional arrivals (historical dispersal), rather than regular (ecological/population recruitment). Nothing explicit is known, though there may be some of both – some cohort-scale recruitment may take place, at times.

Some of the diadromous species that are absent from the Chathams are those that are also lacking or sparse in western Fiordland southern Southland and Stewart Island, so it is possible that some species are more robust migrants, or recruit back to fresh water more successfully than others. However, there may also be some purely stochastic issues relating to how many larvae of these species are living in the seas around New Zealand and available to be transported in ocean currents. Maybe it is the species with the higher numbers of larvae in New Zealand's coastal seas that are most likely to reach the remote Chatham Islands and invade the streams there. If recruitment is hazardous, it is even possible that the taxonomic composition of species in the streams on the Chatham Islands varies from year to year, depending on which species manage to periodically recruit there, and this may vary across time. At present, we can only speculate.

9.7 Freshwater Fishes on the Auckland and Campbell Islands

The only freshwater fish species definitely known from the Auckland and Campbell Islands is the diadromous koaro (McDowall 1970, 1990). There are records from the mid-nineteenth century of shortfin eel and banded kokopu on “Auckland Islands” by British naturalist John Richardson (1848). Richardson's “Auckland Islands” specimens were collected during the worldwide voyage of the H.M.S. *Erebus* and *Terror*, which visited the Auckland Islands for about 2 weeks in 1840 (Cheeseman 1909). The type specimens of *Gl. brocchus* and *Gl. reticulatus*, two species based on specimens collected on that visit, are still present in the collections of the Natural History Museum in London, so there is no uncertainty about the identifications of the fish involved – they are banded kokopu (*Gl. fasciatus*)

(McDowall 1970). However, Auckland Islands records of shortfin eel and banded kokopu have never been reconfirmed by later collections, and biologists have been there often (Stokell 1950; McDowall 1970; and museum specimens). Very occasional, recruitment of these species, from mainland New Zealand to the Auckland Islands, perhaps including, coincidentally, at about the time the *Erebus* and *Terror* visited the islands, cannot be totally discounted, with the two species having since disappeared from these very remote, but biologically little-modified, islands.

Alternatively, it is, I suppose, possible that Richardson's fish actually came from islands in the Hauraki Gulf near Auckland city in northern New Zealand, such as Great Barrier and Little Barrier Islands, which could have been referred to as "Auckland Islands, lying in the Hauraki Gulf, not far from Auckland city, and on which several freshwater fish species are known (Table 9.2), rather than from the Auckland Islands in the remote Southern Ocean (see McDowall 1970).

Or, the samples could have been somehow mis-labelled during handling (something that is not unknown, even at the former British Museum (Natural History), now the Natural History Museum (McDowall 2002). What ever transpired, these fish species do not seem to be present on the Auckland Islands now: no additional records of either from the Auckland Islands are available, and they have been visited relatively often, though there has never been any detailed survey of the islands freshwater ecosystems. The presence of both of these species at far southern latitudes is certainly contrary to both being species tending to be more northern in range in New Zealand (as discussed earlier in the section on latitudinal change in the abundance of diadromous species) (see Fig. 9.6).

9.8 Elevation and Inland Penetration in Diadromous Species

Diadromous species migrate into New Zealand's river systems from the sea, occasionally as mature adults (anadromous species such as lamprey, common smelt and Stokell's smelt), but more often as small juveniles (amphidromous and catadromous species – see Table 1.1). The pattern of invasion of these fishes has several consequences for plots of frequency of occurrence which (whether viewed in strata of 10 m elevation or of 10 km inland penetration), exhibit similar broad overall patterns of variation among the species.

- (i) Upstream migration takes place for every individual in all cohorts of diadromous species (with the exception of 'landlocked' stocks).
- (ii) The extent (distance) and intensity (number of sites) of inland penetration varies widely among the species, and each species typically exhibits a broad continuum at declining frequency of occurrence, from coastal/low elevation sites, to those further inland and at higher elevations, across the diadromous fauna.
- (iii) Within that continuum, most diadromous species exhibit their greatest frequency of occurrence at low elevations and close to the sea, and this seems to be true regardless of whether a species' inland penetration is slight (Stokell's

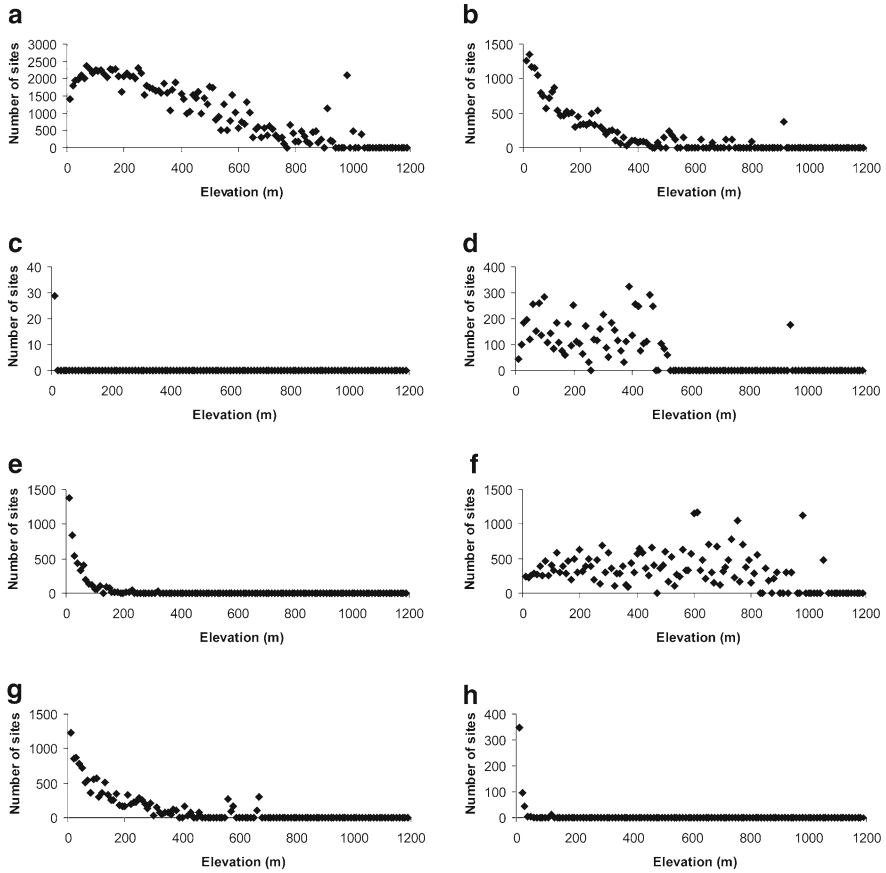


Fig. 9.7 Decline in standardised frequency of occurrence with increasing elevation in selected diadromous species: **a.** longfin eel, *Anguilla dieffenbachii*; **b.** shortfin eel, *A. australis*; **c.** Stokell's smelt, *Stokellia anisodon*; **d.** shortjaw kokopu, *Galaxias postvectis*; **e.** inanga, *G. maculatus*; **f.** koaro, *G. brevipinnis*; **g.** common bully, *Gobiomorphus cotidianus*; and **h.** giant bully, *Gb. gobioides*

smelt – Fig. 9.7c; inanga – 9.7e; giant bully – 9.7h), or is substantial (longfin eel – Fig. 9.7a; shortfin eel – Fig. 9.7b; shortjaw kokopu – Fig. 9.7d or koaro – Fig. 9.7f).

- (iv) Species with low inland penetration tend, also, to be those that prefer slow-flowing habitats (McDowall 1990), and where these species penetrate well upstream, it is usually only in the larger rivers with low gradients in their lower reaches, such as the Waikato, Whanganui, and Manawatu Rivers.
- (v) Where inland penetration is least, as in the species listed in (iii) above, there is always also very rapid, concomitant, decline in frequency of occurrence with increasing elevation/penetration (as in Stokell's smelt – Fig. 9.7c; inanga – Fig. 9.7e; giant bully – Fig. 9.7h). There are no comparable data for actual

abundances of these species, but this will also, predictably, decline rapidly with increasing elevation and distance inland – though again the pattern of decline will vary widely across the fauna and among rivers.

- (vi) These plots of frequency of occurrence are always very strongly positively skewed. In a few instances species with high penetration may be present a little more frequently in strata inland from the coast, rather than in the most downstream stratum (see shortjaw kokopu – Fig. 9.7d; and koaro – Fig. 9.7f). This may reflect the species' preference for streams in hill country and the presence of lowland/coastal plains in some parts of New Zealand, and/or perhaps it may also signify anthropogenic modification of lowland streams, where human population densities and industrial activities are greatest and these species tend to disappear from the most lowland strata, as a result (McDowall 1990).
- (vii) Greatest inland occurrence is seen in longfin eel (Fig. 9.7a) and koaro (Fig. 9.7f); these two species are widely recognised as being adept at climbing even high falls (Harper 1896; McDowall 1990, 2003a). They are also often found in small, sometimes steep-gradient, hill country streams, which tend to be further up stream, though such streams are not necessarily far inland, owing to New Zealand's elongate and narrow shape, its steep, mountainous topography, and the often close proximity of high elevations to the coastline.
- (viii) The shortfin eel is typically recognised as a species that is found most often in low elevation wetlands and estuaries (Figs. 9.4c and 9.7b; Jellyman and Todd 1982; McDowall 1990), and this is reflected in its rapid decline in site frequency with increasing elevation (Fig. 9.7b). But, interestingly (McDowall 1993), shortfin eel may sometimes be found very long distances inland if there are suitable, accessible, inland wetland/lacustrine habitats (as in the Waipa/Waikato River system, at 240 m elevation and 242 km upstream; in the Whanganui River, at 580 m elevation and 307 km upstream; or in Fish Lake in the headwaters of the Wairau River in Marlborough, at elevation >1,000 m and 168 km upstream from the sea). Thus, in some species, inland presence can, in part, be an issue of the availability of suitable habitats at inland sites, as much as their instinct/ability to migrate long distances up stream.

Another perspective is given to these patterns of inland penetration in a dataset of >300 sampling sites in a single river system, the Grey River, West Coast, South Island. Figure 9.8 shows the relative abundance of 12 diadromous species, plotted by species for different distances up stream in this substantial river; clearly, the species present differ greatly in their inland penetration in this river, as they do around New Zealand as a whole. Most species are at, or near, greatest frequency of occurrence in the most downstream sites, and exhibit major differences in penetration, from common smelt demonstrating very little inland penetration, to longfin eels where there is both substantial and frequent penetration. Patterns at the catchment scale in the Grey River (Fig. 9.8) are very much the same as they are at the New Zealand-wide scale.

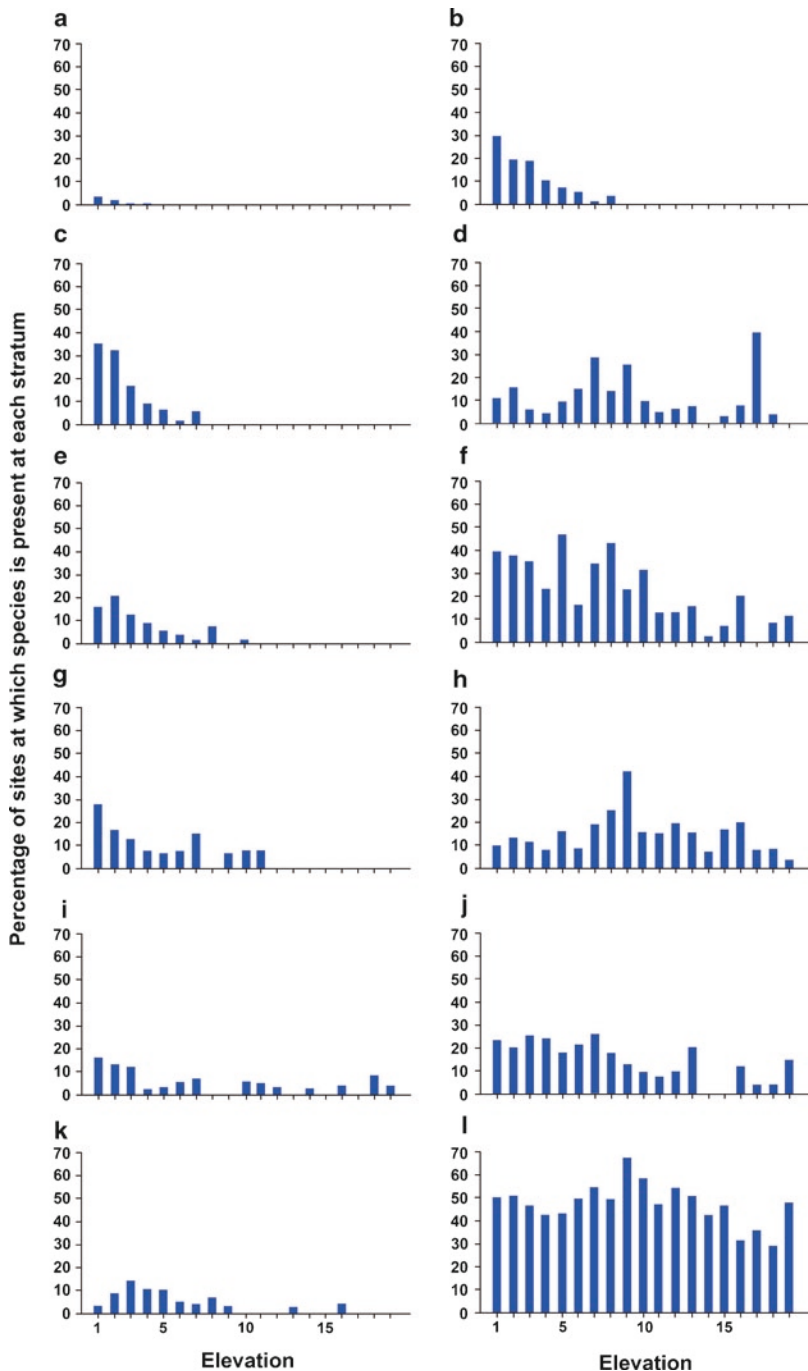


Fig. 9.8 Differences in penetration of 12 diadromous species in the Grey River, West Coast, South Island: **a.** common smelt, *Retropinna retropinna*; **b.** banded kokopu, *Galaxias fasciatus*; **c.** inanga, *Gl. maculatus*; **d.** bluegill bully, *Gobiomorphus hubbsi*; **e.** giant kokopu, *Gl. argenteus*; **f.** redfin bully, *Gb. huttoni*; **g.** common bully, *Gb. cotidianus*; **h.** torrentfish, *Cheimarrichthys fosteri*; **i.** shortfin eel, *Anguilla australis*; **j.** koaro, *Gl. brevipinnis*, **k.** shortjaw kokopu, *Gl. postvectis*; **l.** longfin eel, *A. dieffenbachii*

9.9 Broad-Scale Distributions and Diadromy

What is clear from these various perspectives on distribution patterns discussed above is that diadromous migrations appear to be strongly associated, at several spatial scales, with various features of distribution patterns:

- (i) At a national scale most diadromous species are present vary widely across the latitudes occupied by the New Zealand archipelago (34–47°S latitude).
- (ii) At a regional scale they are present in river systems widely around New Zealand especially at low elevations and penetrations; and there is wide variation among species in the extent of the elevations and distances inland (penetrations) attained, the differences being consistent with informally recognised differences in the ability of species to penetrate rapid water flows and climb barriers (McDowall 1990, 2003a).
- (iii) Species recognised as being strong climbers of falls are typically present in rivers and streams at higher elevations and longer distances inland, especially longfin eel (Figs. 9.4b and 9.7a) and koaro (Figs. 9.4d and 9.7f), but also shortfin eel (Figs. 9.4c and 9.7b), banded kokopu (Fig. 9.4e), shortjaw kokopu (Fig. 9.7d), and, also to some extent, redfin bully (Fig. 9.8f). Some of these species are specially adapted to assist climbing: koaro, at least, have distinctive rugosities on the ventral surfaces of their large, broad, downward-facing pectoral and pelvic fins, this probably being a consequence of the swift water habitats in which they are customarily found, but it probably also assists (pre-adapts) them in climbing (McDowall 2003a); however, in all species, climbing probably depends substantially on the use of surface tension on wetted rock surfaces lateral to the main flows pouring down falls in streams, and it is likely that only small individuals are effective climbers.
- (iv) Some species that are not recognised as climbers may nevertheless penetrate long distances inland, as long as connectivity is maintained in rivers, as instanced by torrentfish, and especially if river gradients are low (McDowall 2000).

There are, of course, many species exhibiting intermediate patterns of occurrence.

9.10 Elevation and Penetration: Differing Patterns in Non-diadromous Species

In earlier discussion in this chapter I drew contrasts between diadromous and non-diadromous species in the breadth of their distributions, based on half degree latitudinal bands across New Zealand (Figs. 9.1 and 9.7). This contrast also emerges when addressing other aspects of the distributions of non-diadromous species, and there is explicit contrast with the numbered discussion paragraphs, above, on the influence of elevation and penetration on the distribution patterns of diadromous species (see previous section):

- (i) Some non-diadromous species (as is true of diadromous species), do have their highest presence at low elevations and close to the sea (e.g., Canterbury mudfish,

see Fig. 9.9d); others, however, do not exhibit high frequency of sites at low elevations, but may variously have their greatest frequencies of occurrence across a varied range of elevations and distances upstream. Since there are no known behavioural/migratory linkages in these fishes involving migration up stream, either from the sea or within river systems, there is logically no likelihood of similar gradients in non-diadromous fish species.

- (ii) There is wide variability in the ‘centres of occurrence’ among the non-diadromous species, which may have peak abundance at all manner of values for elevation and distance inland; site frequency is not consistently positively skewed, as it typically is in diadromous species, and the data may be more or less normally distributed, with highest frequencies around the middle of the species’ altitudinal ranges (upland bully – Fig. 9.9e), or there may be broad variation in species’ frequency of occurrence, as in Canterbury galaxias (Fig. 9.9a).
- (iii) Some non-diadromous species are found only in waters at substantial elevations (upland longjaw galaxias, bignose galaxias – Fig. 9.9b; Tarndale bully – Fig. 9.9f).
- (iv) In some instances the range of elevations occupied is broad (Canterbury galaxias – Fig. 9.9a; Taieri flathead galaxias – Fig. 9.9c), whereas in other instances it is very narrow (as in bignose galaxias – Fig. 9.9b, and Tarndale bully – Fig. 9.9f).

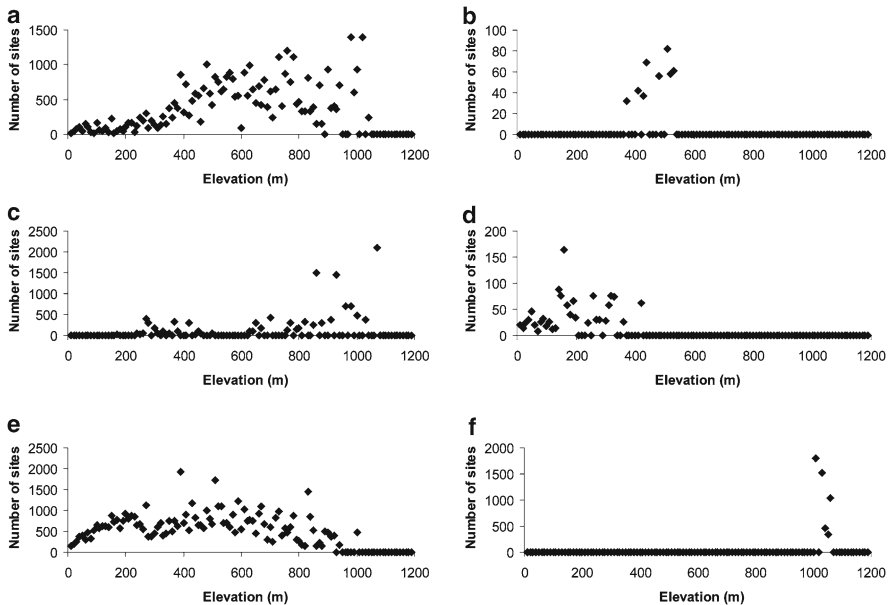


Fig. 9.9 Changes in standardised frequency of occurrence with increasing elevation in selected non-diadromous species: **a.** Canterbury galaxias, *Galaxias vulgaris*; **b.** bignose galaxias, *Gl. macronasus*; **c.** Taieri flathead galaxias, *Gl. depressiceps*; **d.** Canterbury mudfish, *Neochanna burrowsius*; **e.** upland bully, *Gobiomorphus breviceps*, and **f.** Tarndale bully, *Gb. alpinus*

- (v) There is sometimes what looks like a bimodal or fragmented species' range distributions across elevation/penetration; this is, possibly, simply a result of the vagaries of habitat availability/suitability and the ability of species to reach such habitats by dispersal within and between streams (McDowall 1990; Allibone and Townsend 1997) (e.g., Taieri flathead galaxias – Fig. 9.9c); some of the observed patterns of distribution may, however, be driven partly by the fragmentation of populations resulting from the adverse impacts of very widely present, predatory introduced brown trout (*Salmo trutta*) (Townsend and Crowl 1991; McDowall 1968b, 2003b, 2006).

Issues of the patterns of upstream 'penetration' to reach rearing habitats at the cohort scale do not apply to non-diadromous species because they typically spawn in or near normal adult habitats, and there are no known, explicit, patterns of migration (other, perhaps, than some local-scale upstream movements by adults or juveniles that compensate for downstream displacement of larvae in river flows – Cadwallader 1976). However, as discussion below will explore, distribution patterns of non-diadromous species relate closely, at the catchment/regional scale, to a series of geomorphological, volcanic, and climatic events in New Zealand's past history, often relatively recently (at least at a broad, geological, time scale).

9.11 Some Features of Ranges

The concept of species' ranges is used widely in both ecological and historical biogeography, and is often compared across taxa or geographical areas. Questions of species' range characteristics and range sizes have occasioned considerable discussion among macroecologists (Caughley et al. 1988; Gaston 1990, 1991; Brown et al. 1996; Gaston and Blackburn 1999; McGeoch and Gaston 2002; Gaston 2003, and references therein). Even the superficially simple question of how to define a species' range has caused considerable debate, quite apart from attempts to determine widely applicable generalisations that connect range size and shape to other aspects of species' abundance, ecology, distribution, and biogeography.

Brown et al. (1996) summarised that geographic range is the "manifestation of complex interactions between the intrinsic characteristics of organisms ... and the characteristics of their extrinsic environment" which, I suppose, simply means that species live where they can get to (in terms of historical range expansion) and where they can survive (as a result of contemporary habitat suitability and range limitation)! Brown et al. (1996) also reckoned that many of the characteristics of the ranges of species, and also of multispecies, monophyletic, clades, including the size, shape, boundaries, and internal structure of ranges, are affected by both the history of place and the history of lineage, i.e. that ranges, on the one hand are an outcome of the historical processes leading to integration of a species' preferences or tolerances and, on the other hand relate to the colonisation (ecological) processes that have allowed species to spread into their existing ranges, and to persist there. Also, it seems certain that species must have often undergone substantial range shift across geological time

scales as a result of climatic variation, e.g., New Zealand species would have been excluded from higher elevation sites by reductions in temperatures and/or the advance of glacier ice down the big intermontane valleys of the Southern Alps, and perhaps until quite recent times – they could not have persisted in the valleys when they were ice filled, as they were at times of climatic cooling and the advance of glaciers. Equally, they clearly must have spread back up stream/up slope in the rivers of the intermontane valleys to reach contemporary habitats as temperatures rose during interglacial periods, much as they are at present. These kinds of movement probably happened repeatedly through the prolonged period of major climatic fluctuations associated with the Pleistocene glaciations, though there is no way of being certain, or of quantifying the movements. Thus, the ranges of species, that we are able to observe today, are a kind of integration of historical and contemporary ecological patterns. Moreover, what we can observe now may be neither ancient nor enduring – patterns are very dynamic and forever responding to geological and climatic changes.

It is of some interest that although some species, such as Canterbury galaxias, alpine galaxias and upland bully have apparently managed to re-invade the Waimakariri River which drains the eastern flanks of the Southern Alps in mid-Canterbury, upland longjaw galaxias has not done so (see Fig. 12.3, ↑), even though all of these species have re-occupied other intermontane valleys, such as the Rakaia, Rangitata and Waitaki Rivers, further south along the Southern Alps.

Gaston (1990) lamented the small number of species for which there is detailed information on global range. This lack of detail seems likely, among other things, to be in part inversely proportional to the breadth of the area of geographical interest – highly localised species are often easier to map accurately. Also, conservationists may tend to take more interest in the distributions and abundances of more localised species, for several possible:

- (i) Partly owing to the narrow ranges being more easily defined and mapped.
- (ii) Perhaps, also, because species with narrow ranges being vulnerable to threat, deriving simply from their narrow ranges, and so may attract more conservation attention.

Localised endemics often seem to gain more than their share of conservation interest, especially if they are seen as relictual, or ancient, or idiosyncratic, either geographically or taxonomically, or if they are thought to be more seriously at risk because of their narrow ranges. Sometimes the more rare and local are also more ‘interesting,’ simply because of their rarity.

Data available on New Zealand freshwater fish species present at >20,000 sites in the NZFFD (see Chapter 6) facilitates the examination of some of the above generalisations, applied to species’ ranges, across the areal span of New Zealand. I have already discussed, above, the fact that diadromous New Zealand freshwater fishes in general have much broader latitudinal ranges than non-diadromous species. This is a rather coarse measure of range, though it is not entirely inappropriate for addressing a series of questions in relation to latitude, owing to New Zealand’s long, slender shape, and near north-south geographical orientation. Also perhaps important is the presence of strong environmental gradients along the north/south

axis of New Zealand that influence ambient temperatures and climate in general, across 13° of latitude.

There is a strong tendency for the number of geographical data points in the NZFFD to correlate negatively with both elevation and penetration, i.e., there are far more sampling sites in the database at lower elevations, and closer to the sea than there are at higher elevations and further inland (Fig. 9.5, 9.9). As discussed earlier, this is owing primarily to the easier physical (human) access to such sites for sampling, but perhaps it also relates to greater conservation attention being paid to low-land sites because of the more intensive human utilisation/modification of low elevation and flat landscapes for farming, industry or human settlement. This is perhaps, in turn, a consequence of anthropogenic impacts deriving from activities like deforestation, wetland drainage, impoundment, water abstraction, density of human population, and pollution, all of which have happened more at lower elevations for a variety of reasons. This has implications among species for comparisons of ranges.

For interspecific comparisons, if the number of sites where a species is found is used as a simple surrogate for range, this could result in species that are found primarily at lower elevations appearing to be relatively more widespread than those occurring at higher elevations. To determine whether that tendency critically distorts our understanding of species' distributions, I explored distribution patterns based on the number of grid squares across New Zealand that species occupy. A plot of the number of sites from which species have been recorded in the NZFFD against the number of 10 km grid squares in which they are found (not shown), exhibits a very close relationship between the two variables. This suggests that the number of sites is about as good as number of grid squares occupied as an overall measure of range size, i.e. number of sites is probably a relatively good approximation of how relatively widespread individual species are.

Several 'rules' have been derived about species' ranges that are variously applicable to the New Zealand freshwater fish fauna as a whole. One such 'rule' is that range size varies with the scale at which it is examined, which is, or is nearly, tautological.

Brown et al. (1996) recognised that features of life history strategies may influence range size, and they pointed to observations that marine mollusc species that have relatively long-lived planktonic (easily dispersed) life stages tend to have broader ranges than those that don't. This is generally true of marine invertebrates, for example (Thorson 1950; McDowall 1968a). Sherman et al. (2008) discussed this issue for marine invertebrates in general, finding that groups with plankton-living larvae have much greater potential for dispersal by ocean currents compared to those with direct development, which tend to have highly philopatric distributions. This rather mirrors observations presented here that diadromous species, with oceanic, often pelagic/planktonic juveniles, tend to have broader geographical ranges than non-diadromous ones. Diadromous fishes, and marine species with enduring planktonic larvae, are both likely to have higher dispersibility, and for the same reasons (Booth and Ovenden 2000; Burridge et al. 2006; Waters 2007).

Brown et al. (1996) discussed how the sizes of species' ranges, when summarised across a group of taxa, tend to be strongly right skewed, i.e., many species

have small ranges and fewer have very large ones. However, if latitudinal range is taken as a surrogate for range size, then data I have presented above show that this is not true of New Zealand's freshwater fishes as a whole, in which range sizes in the total fauna are bimodal. On the one hand, many diadromous species have large ranges and many fewer have smaller ranges, contrary to Brown et al.'s prediction. On the other hand, range size in non-diadromous species is, as predicted by Brown et al. (1996), positively skewed, and most species having small ranges. This metric, range size, thus subdivides the fauna, yet again, on the basis of life history strategy (see Figs. 9.2 and 9.3, which separate diadromous and nondiadromous species). Viewing the fauna as a whole, the generalisation of Brown et al. (1996) that most species have small ranges does not hold.

Brown et al. (1996) also suggested that there is a phylogenetic component to range size, with closely related species tending to have more similar ranges than those of disparate ancestry, thinking that: "This suggests that intrinsic characteristics of the organisms inherited from their common ancestors influence the ecological interactions that limit geographic distributions." This seems, to me, a strange notion and seems contrary to the idea of local isolates of widespread taxa diverging and speciating. Among New Zealand's freshwater fishes there seems to be little association between range size and how closely related taxa are – the greatest similarities are among those that either are, or are not, diadromous, and so range size relates, once again, to life history strategies rather than to a shared ancestry.

Derivation of non-diadromous species from diadromous species is commonplace in the phylogenetic history of New Zealand's freshwater fish fauna (McDowall 1970, 1988, 1990; Waters et al. 2001; Waters and McDowall 2005; Stevens and Hicks 2009). And, as the diadromous/non-diadromous dichotomy cuts across many monophyletic species groups, there is no explicit segregation of fish species, in terms of their range size, that relates to phylogeny – and this applies even among closely related non-diadromous species. Rather, there are repeated instances of non-diadromous species with very narrow distributions (localised endemics) having closest affinities with diadromous species that are broadly distributed.

Furthermore, sometimes the narrow ranges of species lie geographically within the broader range of sister taxa, as demonstrated in this paper in the discussion of pattern in various species groups, e.g. burgundy mudfish (see Fig. 14.3 – arrow 20, purple symbols) compared with black mudfish (see Fig. 14.3 – black symbols); bignose galaxias (see Fig. 12.2 – red symbols) and lowland longjaw galaxias (see Fig. 12.3 – yellow symbols) compared with other species in the pencil-galaxias species group (see Figs. 12.2 and 12.3); Teviot galaxias (see Fig. 11.3 – yellow symbols) compared with others of the *Gl. vulgaris* species complex; dune lakes galaxias within the range of inanga; or Tarndale bully, compared with upland bully (see Fig. 15.2 – green symbol and blue symbols). Here we are seeing repeated instances of localised speciation and narrow ranges *within* the broader ranges of related species.

The 'phylogenetic argument' (Brown et al. 1996) seems to break down as there is no explicit sense in which at least some of the non-diadromous species are necessarily, mutually, more closely related to each other, rather than each is related to any diadromous species. Thus, the flaw in Brown et al.'s generalisation about the phy-

logenetic component of range size, at least as it applies to New Zealand's freshwater fishes, is that closely related species do not necessarily have more similar life histories and ecologies. Or, putting it another way, life history strategies tend often to group species very differently from groups based on phylogenetic relationships and a shared ancestry. To the extent that speciation processes are peripatric (Mayr 1982; Mayr and Diamond 2001), it would seem predictable that establishment of localised derivative species in pockets around the periphery of widespread ancestral species would be routine rather than exceptional. Widespread diadromous species seem almost preadapted to providing the foundations for proliferation of derived species with restricted geographical ranges, often around the fringes of their ranges, or locally evolved by 'landlocking' in diadromous species.

9.12 Range Size in Fluvial Habitats

Compared with terrestrial or oceanic habitats, freshwater habitats (both rivers and lakes) tend to be especially discontinuous or fragmented, making it difficult for species to occupy the entire extent and diversity of suitable habitats across a broad landscape – freshwater fishes tend to be extreme instances in which the taxa comprise complex and highly fragmented metapopulations. This is especially true of New Zealand with its very numerous, mostly small, separate, river systems (there are >300 major separate estuaries around the long New Zealand coastline (McLay 1976). In *non-diadromous* species, however, distributions are plainly limited by topographical and geological history and, where habitats are highly discontinuous or fragmented, by problems of access to the separate units in these fragmentary habitats. Species are found in places to which they have been able to spread, *and* where there have continuously been suitable habitat conditions over past-to-present history. Typically, changing riverine connections across a landscape are needed to ensure the broad spread of freshwater fish species. Though there are instances of this, it is rare both spatially and temporally, and is discussed for various species groups in later chapters (Chapters 11–15).

The situation is quite different for *diadromous* species – whose broad freshwater ranges are facilitated by their ability to move between isolated river/lake systems through coastal seas, though ranges at the 'within catchment' scale are constrained by their ability to penetrate upstream into river systems from the sea. Thus, range in diadromous species is then not a product entirely of proximate habitat suitability, at all, but is generated by a combination of habitat suitability, habitat connectivity, and the varying ability of individuals of the species to penetrate upstream to reach these habitats. The maintenance of these distributions must be viewed, for diadromous species, at narrow, cohort-level, proximate, temporal scales, despite most of the diadromous species being very widespread.

Goodwin et al. (2005) argued that most fish have narrow ranges. What 'narrow' means in this context is not clear, and it is clearly a matter of perspective. Viewed at the 'New Zealand' scale, there is a distinct dichotomy in range size, with about half

the fauna (the diadromous species) have consistently broader ranges than their non-diadromous counterparts. In that sense many of the species have broad ranges.

Caughley et al. (1988) defined the “edge” of a species’ range as the “zero-density resultant of conditions being not quite good enough [and being] ... where mortality from abiotic (i.e. density independent) sources balances fertility”. This, of course, presupposes that a species’ range relates closely to the locale of its reproductive output, or juvenile recruitment (which is often untrue, especially in the case of diadromous fish species). It also assumes that the individuals of the species are able to reach an edge that is ecologically limiting and, especially for freshwater fish, they may not be able to – unless the edge is viewed as the land/freshwater interface, and I don’t think that was what Caughley et al. (1988) were alluding to. Moreover, it also depends on whether the ecological factors that are controlling species’ abundance also influence reproductive success/juvenile recruitment, and, again, in diadromous species in particular, this may not be so: both may be controlled very substantially by conditions/processes that are geographically remote from adult/reproductive habitats. Otherwise, Caughley et al.’s (1988) definition seems essentially tautological, though is perhaps useful from an ecological perspective.

In the freshwater biome, the idea that individuals of a species can spread no further than the edge of the habitat body in which they are living might *seem* so simplistic as to not require mention for rivers and lakes, but is that so? Even when broad-scale range patterns of species are an outcome of historical-scale influences (speciation patterns and geological/climatic events), it nevertheless remains true that at the local scale (however defined) distribution is profoundly influenced by ecology. It is a question of high discontinuity of freshwater habitats that are, in some ways, comparable to the terrestrial biome discontinuities characteristic of oceanic islands. Brown et al. (1996) recognised that ranges may be “limited by history rather than ecology”, but that, too, is only partly true for diadromous species – in the sense that their ranges, at least in fresh water, are not an ultimate/historical feature so much as a proximate/ecological one (or a behavioural one, to be precise). It is all rather more complex, but clearer, for diadromous species.

Brown et al. (1996) thought that most studies “have found that species with smaller ranges are consistently confined to the tropical end of a latitudinal gradient or the shallow end of a depth gradient.” To the extent that the c. 13° of latitude represented by New Zealand can be called a latitudinal gradient, Brown et al.’s (1996) summary statement is inapplicable for freshwater fish. Among diadromous species there is no latitudinal gradient of range size, at all, since all but two of them are found across almost the entire latitudinal extent of New Zealand. And for non-diadromous species, the narrowest ranges are primarily an outcome of the location of historical processes of allopatric speciation and lineage splitting, and this seems unrelated to latitude. Here and there, widely across the New Zealand landscape, are small pockets where there are species with very narrow ranges, again, as discussed in detail later in this paper, for:

- (i) Burgundy mudfish (see Fig. 14.3 – purple symbols, arrow 20) and dune lakes galaxias (see Fig. 13.2 – red symbols) in the far north.

- (ii) Tarndale bully in the mountains of inland Marlborough (see Fig. 15.2 – green symbols).
- (iii) Bignose (see Figs. 12.2 and 12.3 – red symbols) and lowland longjaw galaxias (Figs. 12.4 and 12.4 – yellow symbols) both largely in the McKenzie Basin and extending down the Waitaki River.
- (iv) Teviot galaxias, essentially in the upper reaches of the Teviot River, and across the divide to the north in headwaters of the Taieri River (Red Swamp Creek) (see Figs. 11.3 – arrow 14, 11.4, arrow 3 – yellow symbols).
- (v) Eldon's galaxias (see Figs. 11.2 and 11.4 – light blue symbols) and dusky galaxias (see Figs. 11.3 and 11.4 – black symbols) largely in the Waipori and lower Clutha River valleys.
- (vi) Chatham mudfish in two lakes of the southern sector of Chatham Island (see Fig. 14.3, arrow 21).

The implication of these localised distribution patterns is that range size, in these species at least, is determined as much (or more) by history than by ecology, i.e., by local geographical isolation and speciation processes. “Rapoport's rule” (Rapoport 1982), that range size tends to decrease with increasing latitude is generally inapplicable.

9.13 Range Shape

Brown et al. (1996) also discussed range shape. It seems to me unsurprising that they found that differences in range shape were more striking than their similarities, some range shapes being “compact and globular” (did they mean circular?) whereas others are long and attenuated. These differences seem a predictable consequence of interactions between where a species evolved and where it has spread to, and of species' habitat preferences and how these preferences are met/distributed in space.

There is, yet again, a dichotomy in the New Zealand freshwater fish fauna in the shape of the ranges occupied by fish species. For the diadromous species, whose distributions are locked into an association with coastlines and inland penetration (cohort-scale migrations) up river systems from the sea, ranges are best described as ‘ring ranges’ – these species' ranges consist of bands around the coastal land margins of New Zealand. Virtually all diadromous species have ring ranges, being present from sea-level/coastlines (Fig. 9.4) varying distances upstream in fluvial habitats. Within-species geographical variation in the width of ring ranges may relate substantially to how steep the local-scale topography is, i.e., band width of the ring ranges will tend to be narrower in topographically steep terrain where inland penetration is more difficult, but wider where terrain is less steep and access to upstream reaches easier. Fairly obviously, too, the band width of the ring ranges of diadromous species will have downstream-upstream dimensions (band width) determined by the distances each species is capable of penetrating upstream from the sea within each river system. Weaker migrants have narrower and lower-elevation ring ranges compared

with stronger migrants. I have found no discussion of the phenomenon of ‘ring ranges’, though Brown et al. (1996) did recognise that when a boundary coincides with a coastline, species abundances may be relatively high “right up to the coast rather than decreasing as the boundary approaches”. This certainly applies to New Zealand’s diadromous freshwater fishes. In a way this is no more than a special case of a more general truth that abrupt and major changes in physical parameters, such as occur especially at biome margins, cause rapid and major changes in the abundances of species (Caughley et al. 1988). Beck and Kitching (2007) concluded that dispersal, “the process of reaching a new site and successfully establishing a population there, is intimately related to realized ranges; they were referring to historical dispersal processes, but, again, with diadromous species it is a dynamic cohort-scale circumstance, and it happens to every cohort of progeny.

Among the New Zealand freshwater fishes we again encounter a fundamental dichotomy between the distributions and range characteristics of species with diadromous or non-diadromous life histories. Someone addressing distributions and range characteristics of New Zealand freshwater fishes would be faced with considerable confusion if ignorant of the life history and dispersal dichotomies exhibited by the fauna. Gaston (2003) cited Hesse et al. (1937), and in doing so presumably agreed with them, that: “Limited range for species and genera is on the whole, a much more general phenomenon than wide distributions”. This generalisation is, once more, negated by diadromous species having wider ranges than non-diadromous species in the New Zealand freshwater fish fauna, and it needs to be remembered that about half that fauna is diadromous.

As a general rule, it seems to me likely that range shapes in fluvial freshwater fishes, and especially in the New Zealand taxa, are likely to be idiosyncratic. Partly this is an outcome of rivers having long and slender shape, as well as each river catchment being highly isolated from others – which means that species’ ranges typically comprise a series of highly isolated sub-ranges (or an extreme version of highly fragmented metapopulations). On top of this, however, New Zealand rivers tend to flow in east-west directions owing to a combination of the archipelago’s long and slender shape, and the near north-south orientation of mountain ranges, this, in turn, being a product of the interaction of the Australian and Pacific tectonic plates that are generating the uplift of the mountain ranges (see Section 3.3). The outcome of this is the tendency for gradients in key environmental features, especially temperature, to have complex orientations relating to both latitudinal and altitudinal gradients. Little is known about the role of temperature in determining distribution patterns of New Zealand’s freshwater fish, though some data suggest that species have differing upper temperature tolerances (Simons 1984; Richardson et al. 1994). The restriction of some (always non-diadromous) species to higher elevations (Fig. 9.9) may be an outcome of preferences for lower temperatures, but it could also relate to competition (about which nothing is known). Fish communities are more speciose at low elevations – at least as regards what can be observed today, recognising the adverse and broad-scale impacts of introduced, predatory salmonids (McDowall 2003b, 2006).

There is no latitudinal change in species’ range sizes among diadromous species since virtually all of them are widely present from north to south across New Zealand.

Nor is there much evidence for latitudinal variation of range size in nondiadromous species, which may have narrower, most of them *much* narrower, ranges than diadromous species. Their ranges probably relate substantially to local speciation processes, and to contemporary topography and climate across the landscape, rather than to New Zealand's earth history.

9.14 Patterns of Species Richness in the Fauna

Species richness is a measure of the number of species present in a designated region or habitat. Local species richness depends greatly on regional species richness as the latter forms the pool of species available to contribute to local species richness (Gaston and Williams 1996; Brooks and McLennan 2002). Local species richness also depends substantially on the scale at which it is measured – the finer the scale, the lower the species richness.

9.15 Latitudinal Variation in Site Species Richness

One of the direct and explicit implications of the very broad, north-south, latitudinal ranges of the diadromous species (Figs. 9.1 and 9.1), and their numerical dominance throughout the latitudes of New Zealand, is that there is relatively little latitudinal variation in species richness. This can readily be estimated from the plot of distributions of species in half-latitude bands shown in Fig. 9.1. The number of diadromous species per half latitude band may be as low as 10, but in general is relatively stable at 14–16 species per band – see the horizontal row of numbers below the upper panel in Fig. 9.1; 56–90% of the species in each half degree latitudinal band are diadromous. Not only is the number of diadromous species relatively high and stable across the latitudinal range of New Zealand, but also, in general, more than three quarters of the 17 diadromous species in the fauna are present in each band, i.e., it is much the same group of diadromous species that contributes substantially to species richness across the range of latitudes. Differences in overall species richness between bands are due substantially to variation in the number of non-diadromous species present, and especially to the higher number of non-diadromous species in the southern South Island.

Species richness values are a little lower in the northernmost and southernmost $\frac{1}{2}^\circ$ latitudinal bands (10–11 species, or c. 59–66% of species: Fig. 9.1). Lower values in the far north of Northland may be due to the 'peninsula effect' (a tendency for species richness to decline on long narrow peninsular land areas – Simpson 1964; Jenkins and Rinne 2008), though this might seem less likely to influence diadromous fish species richness, because these species can disperse widely through coastal seas as a corollary of their life histories). Lower species richness in rivers of Stewart Island, in the far south, may simply result from less intensive

sampling there (only 52 sites). Some of the latitudinal variation may be due to some species being less widely present in northern localities, perhaps being cold water species (lamprey – Fig. 9.6a and koaro – Fig. 9.6a, d), or others rarer in southern localities, because of a preference for warmer temperatures (shortfin eel – Fig. 9.6b and banded kokopu) (see Fig. 9.6c).

The pattern of latitudinal variation in species richness for non-diadromous species is quite different from that in diadromous species – richness being always relatively low (compared with communities dominated by diadromous species), and exhibiting latitudinal variation. As well, different combinations of non-diadromous species are contributing to the species richness along the length of New Zealand. A slight increase in species richness towards southern New Zealand is contrary to the often-cited tendency for complex tropical and sub-tropical ecosystems to be more diverse than those at higher latitudes (Stevens 1989; Gaston and Williams 1996; Cardillo 2002; Willig et al. 2003; Hillebrand 2004), though it might be argued that there is insufficient latitudinal range in New Zealand (c. 13°) for this generalisation to be applied to the fauna, and the difference is minor. What ever is the explanation of global patterns in species richness, the somewhat higher richness in southern New Zealand probably has historical rather than ecological significance – it is driven substantially by the availability of geologically-enduring southern landscapes in which the fauna has evolved and diversified, combined with the post-Oligocene disruption of the landscape by mountain building, marine transgression, uplift, glaciation, volcanism and other historical events elsewhere across New Zealand. Specifically, southern New Zealand, where species richness of non-diadromous species is greatest, represents a relatively large, more ancient, and possibly more stable, landscape than much of the rest of New Zealand (Fleming 1979; Cooper and Cooper 1995; Gibbs 2006) (Fig. 3.2), if any landscape at all survived the Oligocene drowning episode (Landis et al. 2008) – the southern South Island is certainly an area of elevated endemism in other taxonomic groups as well.

9.16 Species Richness at the Catchment Scale

Species richness of diadromous species in any New Zealand river system is virtually always greatest at low elevations and close to the sea, and there is a consistent downstream-upstream decline in species richness from river mouths. This change in species richness runs parallel to changes predicted by the River Continuum Concept (RCC – Vannote et al. 1980), though the causation is quite different (McDowall 1998) – the trajectories of change in New Zealand rivers need to be viewed as downstream-upstream processes, driven by invasion of diadromous fish from the sea, and taking place at the cohort scale (rather than the upstream-downstream processes postulated by the RCC that functions at the community scale). Species richness of non-diadromous species, however, is often greatest at higher elevations and there is no consistent decline from sea level/river mouths, upstream.

9.17 Site Species Richness

Site species richness varies widely across the fauna. However, consistent with the relatively low species richness at the national level, compared with many other lands, and especially the generally small number of non-diadromous species throughout New Zealand, species richness in New Zealand freshwater fish communities is also never high by global standards of comparison. No species were recorded from nearly 2,000 sites (c. 10%). Maximum recorded site species richness is 12 species, less than 100 sites among c.15,000 NZFFD sites not associated with lakes had eight or more species present, and there are rarely more than about six. And, also consistent with a large proportion of the fauna being diadromous, combined with widespread latitudinal ranges of diadromous species and narrow latitudinal ranges of non-diadromous species, site species richness is widely dominated by diadromous species. Their contribution is typically much higher than their c. 43% contribution to the total fauna.

Another way of viewing species richness is to examine how this varies across river systems and, specifically, in relation to distance upstream from river mouths and across increasing elevations. Again, I have partitioned diadromous and non-diadromous species. Figure 9.10 shows average site species diversity across a range of distances inland and elevations for c. 15,000 sampled sites (again only those sites not associated with lakes), with the data stratified at distances of 5 km intervals

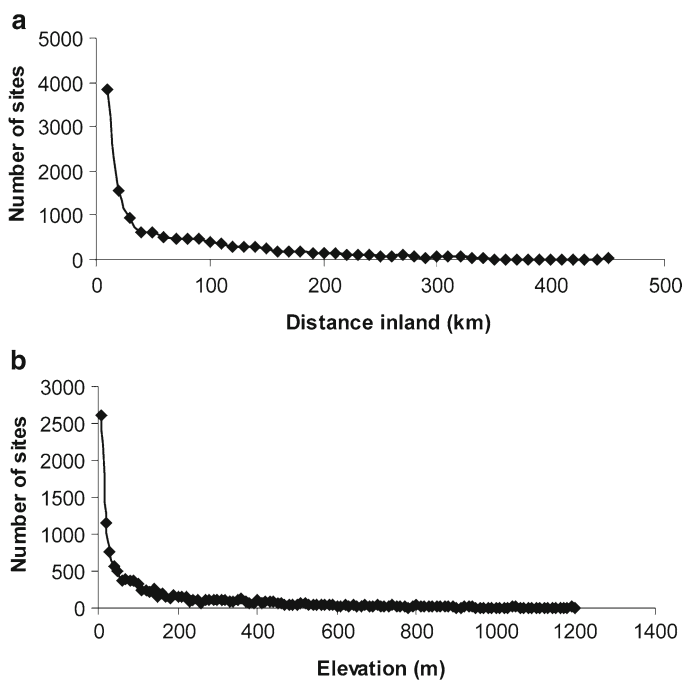


Fig. 9.10 Changing number of NZFFD sites with: **a.** increasing distance inland; **b.** increasing elevation

inland and 10 m elevation. The number of sites sampled decreases rapidly with distance inland and elevation (Fig. 9.10) Partly because of New Zealand's steep topography and the proximity of elevated landscapes close to the sea, there is common occurrence, at low elevations, of habitats suited for species that favour steep, swift-flowing bouldery streams, i.e., though this may seem counterintuitive, steep, swift-flowing, bouldery streams are widely available at low elevations in many parts of New Zealand. The rate of inland decline of each species' presence is a reciprocal of a measure of the steepness of the topography and the tendency/ability of each species to penetrate upstream.

For plots of both distance inland and elevation, species richness for diadromous species is highest at the lowermost sites, and declines rapidly with distance/elevation (Fig. 9.11). This is, of course, entirely in accordance with several metrics.

- (i) Widespread latitudinal range of diadromous species so that most species are present at all latitudes.

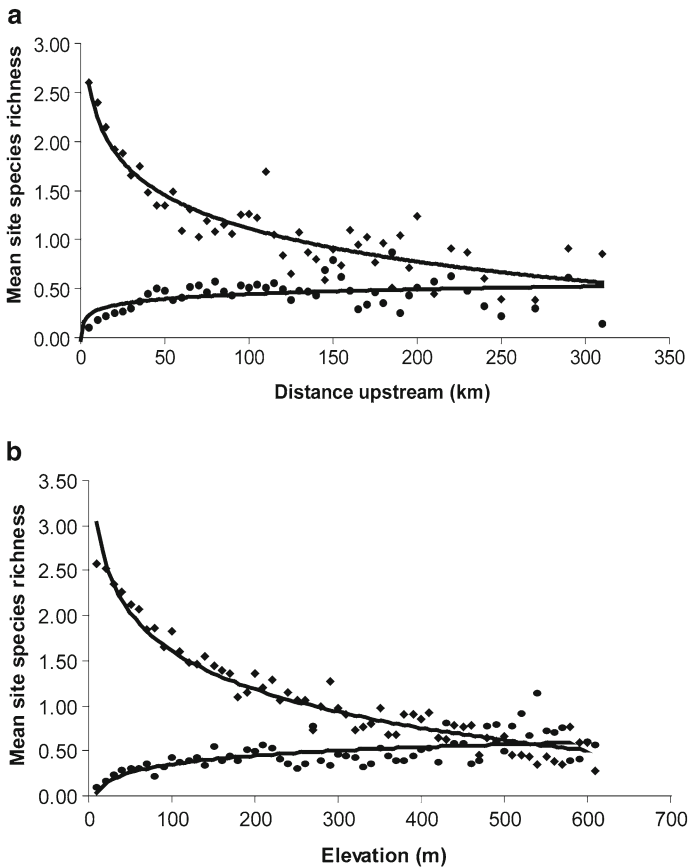


Fig. 9.11 Varying site species richness with: **a.** increasing distance upstream and **b.** increasing elevation for diadromous species (♦) and non-diadromous species (●)

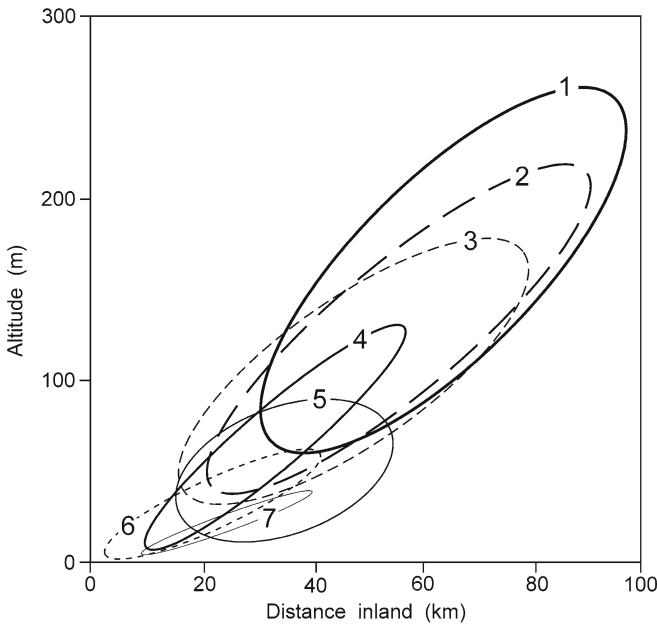


Fig. 9.12 Changing species richness with increasing distance from the sea coast for diadromous species in the Grey River, West Coast, South Island, based on 320 sites (Gaussian ellipses enclose 50 % of distributions at each level of species richness – numeral in ellipse)

- (ii) Diadromous species typically having continuous downstream-upstream distributions within river systems, extending from the sea coast, inland.
- (iii) Their often having greatest frequency of occurrence near river mouths, and almost always declining abundance from downstream to upstream.
- (iv) Great variation among species in the extent to which each penetrates inland.

Figure 9.12 displays downstream-upstream change in site species richness for diadromous species in fish communities in the Grey River on the West Coast of the South Island, and represents data from 320 sites (McDowall 1998). The Gaussian ellipses enclose 50% of the sites at each richness level, and exhibit clear decline in site species richness with increasing elevation and distance inland (upstream penetration). The ellipses collapse more rapidly towards the penetration (X) axis than the elevation (Y) axis, especially at high species richness, perhaps suggesting that elevation influences upstream migration more strongly than penetration.

9.18 Nestedness

Nestedness is a characteristic of biotas in which smaller assemblages of species form subsets of successively larger assemblages. It can be generated by diverse environmental and behavioural attributes including colonisation, extinction, or

environmental gradients. Cook et al. (2004) refer to “progressive addition of species to local assemblages as stream size increases”, citing Sheldon (1968), and Angermeier and Schlosser (1989); it is also a prediction of the river continuum concept of Vannote et al. (1980), which seeks to provide a mechanistic explanation related to upstream/downstream gradients in resources and biotas of rivers. I have not calculated nestedness indices for the New Zealand freshwater fish fauna, though it is plainly evident that the downstream-upstream gradients of declining species richness in diadromous species, driven by one species after another ‘dropping out’ of the communities with increasing elevation or penetration, will result in a form of nestedness, though it needs to be seen as ‘progressive loss’ rather than ‘progressive addition.’ Cook et al.’s (2004) suggestion that “Nestedness arises when a gradient in species traits is juxtaposed on an important environmental gradient” is upheld by what we know of the penetration/colonisation attributes of diadromous (especially amphidromous and catadromous) fishes, the relevant species’ traits being upstream migratory ability and instinct.

References

- Allibone RM, Townsend CR (1997) Reproductive biology, species status and taxonomic relationships of four recently discovered galaxiid fishes in a New Zealand river. *J Fish Biol* 51:1247–1261
- Angermeier PL, Schlosser IJ (1989) Species area relationships for stream fishes. *Ecology* 70:1450–1462
- Beck J, Kitching IJ (2007) Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Glob Ecol Biogeogr* 16:341–349
- Booth JD, Ovenden JR (2000) Distribution of *Jasus* spp. (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment. *Mar Ecol Prog Ser* 200:241–255
- Brooks DR, McLennan DA (2002) The nature of diversity: an evolutionary voyage of discovery. University of Chicago, Chicago, IL, 668 pp
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries and internal structure. *Ann Rev Ecol Syst* 27:597–623
- Burridge CP, Melendez R, Dyer BS (2006) Multiple origins of the Juan Fernandez kelpfish fauna, and evidence for frequent and unidirectional dispersal of cirrhitoid fishes across the South Pacific. *Syst Biol* 55:566–578
- Cadwallader PL (1976) Home range and movements of the common river galaxias, *Galaxias vulgaris* Stokell (Pisces: Salmoniformes) in the Glentui River, New Zealand. *Aust J Mar Freshwater Res* 27:23–33
- Cardillo M (2002) The life history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator. *J Anim Ecol* 71:78–87
- Caughley GC, Grice D, Barker R, Brown B (1988) The edge of the range. *J Anim Ecol* 57:771–785
- Cheeseman TF (1909) The systematic botany of the islands to the south of New Zealand. In: Chilton C (ed) *The Subantarctic Islands of New Zealand*. Philosophical Institute of Canterbury, Christchurch, N Z, pp 389–471
- Cook RR, Angermeier PL, Finn DS, Poff NL, Krueger KL (2004) Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia. *Oecologia* 140:639–649
- Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proc R Soc Lond B Biol Sci* 261:293–302
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp

- Gaston KJ (1990) Patterns in the geographical ranges of species. *Biol Rev* 65:105–129
- Gaston KJ (1991) How large is a species' geographic range? *Oikos* 61:434–438
- Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford, 280 pp
- Gaston KJ, Blackburn TM (1999) A critique for macroecology. *Oikos* 84:353–368
- Gaston KJ, Williams P (1996) Spatial patterns in taxonomic diversity. In: Gaston KJ (ed) *Biodiversity: a biology of numbers and difference*. Blackwell Science, Oxford, pp 202–229
- Gibbs GW (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton, Nelson, N Z, 232 pp
- Goodwin NB, Dulvy NK, Reynolds JD (2005) Macroecology of live-bearing in fishes: latitudinal depth range comparisons with egg-laying relatives. *Oikos* 110:209–218
- Harper AP (1896) Pioneer work in the alps of New Zealand: a record of the first exploration of the chief glaciers and ranges of the Southern Alps. Fisher & Unwin, London, 336 pp
- Hesse R, Allee WC, Schmidt KP (1937) Ecological animal geography. Wiley, New York, 715 pp
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:195–211
- Jellyman DJ, Todd PR (1982) New Zealand freshwater eels: their biology and fishery. *N Z Min Agric Fish, Fish Res Div Info Leaf* 11:1–19
- Jenkins DG, Rinne DZ (2008) Red herring or low illumination? The peninsula effect revisited. *J Biogeogr* 35:2128–2137
- Kirk R (1994) The origin of Waihora/Lake Ellesmere. In: Davies J, Galloway L, Nutt AHC (eds) *Waihora/Lake Ellesmere: past present future*. Lincoln University/Daphne Brasell, Lincoln, New Zealand, pp 9–16
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Mayr E (1982) Processes of speciation in animals. In: Barigozzi C (ed) *Mechanism of speciation*. Liss, New York, pp 1–19
- Mayr E, Diamond JR (2001) The birds of northern Melanesia: speciation, ecology and biogeography. Oxford University Press, Oxford, 492 pp
- McDowall RM (1968a) Oceanic islands and endemism. *Syst Zool* 17:346–350
- McDowall RM (1968b) Interactions of the native and alien faunas and the problem of fish introductions. *Trans Amer Fish Soc* 97:1–11
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool, Harv Univ* 139:341–431
- McDowall RM (1988) Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London, 309 pp
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1993) Implications of diadromy for the structuring and modelling of riverine fish communities in New Zealand. *N Z J Mar Freshwater Res* 27:453–462
- McDowall RM (1998) Fighting the flow: downstream-upstream linkages in the ecology of diadromous fish faunas in West Coast New Zealand rivers. *Freshwater Biol* 40:111–122
- McDowall RM (2000) Biogeography of the New Zealand torrentfish, *Cheimarrichthys fosteri* (Teleostei: Pinguipedidae): a distribution driven mostly by ecology and behaviour. *Environ Biol Fish* 58:119–131
- McDowall RM (2002) Provenance and status of *Galaxias smithii* Regan (1905) (Teleostei: Galaxiidae). *J Nat Hist* 36:1129–1134
- McDowall RM (2003a) The key to climbing in the koaro. *Water Atmos* 11(1):16–17
- McDowall RM (2003b) Impacts of alien salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Trans Amer Fish Soc* 132:229–238
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McDowall RM (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Rev Fish Biol Fisher* 16:233–422

- McDowall RM, Mitchell CP, Brothers EB (1994) Age at migration from the sea of juvenile *Galaxias* in New Zealand (Pisces: Galaxiidae). *Bull Mar Sci* 54:385–402
- McGeoch MA, Gaston KJ (2002) Occupancy frequency distribution: patterns, artefacts and mechanisms. *Biol Rev* 77:311–331
- McLay CL (1976) An inventory of the status and origin of New Zealand estuarine systems. *Proc N Z Ecol Soc* 23:8–26
- Pillans B, Pullar WA, Selby MJ, Soons JM (1992) The age and development of the New Zealand landscape. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 31–62
- Rapoport EH (1982) *Areography: geographical strategies of species*. Wiley, New York, 269 pp
- Richardson J (1848) Ichthyology of the voyage of HMS *Erebus* and *Terror*. In: *The zoology of the voyage of HMS Erebus and Terror* 11:1–139, Janson, London
- Richardson J, Boubée JAT, West DW (1994) Thermal tolerance and preference of some native New Zealand freshwater fish. *N Z J Mar Freshwater Res* 28:399–407
- Rutledge MJ (1992) Survey of Chatham Island indigenous freshwater fish, November 1989. Department of Conservation, Christchurch, N Z, 21 pp
- Sheldon AL (1968) Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193–198
- Sherman CDH, Hunt A, Ayre DS (2008) Is life history a barrier to dispersal? Contrasting patterns of genetic differentiation along an oceanographically complex coast. *Biol J Linn Soc* 95:106–116
- Simons M (1984) Species specific responses of freshwater organisms to elevated water temperature. *Waik Vall Auth Tech Publ* 29:1–17
- Simpson GG (1964) Species diversity of North American mammals. *Syst Zool* 13:57–73
- Skrzynski W (1967) Freshwater fishes of the Chatham Islands. *N Z J Mar Freshwater Res* 1:89–98
- Smith PJ, McVeagh SM, Allibone R (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Stevens G (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. *Am Nat* 133:240–256
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Stokell G (1950) Freshwater fishes from the Auckland and Campbell Islands. *Cape Exped Ser Bull, N Z Dep Sci Ind Res* 9:1–8
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25:1–45
- Townsend CR, Crowl T (1991) Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout. *Oikos* 61:347–354
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. *Can J Fish Aquat Sci* 37:130–137
- Waters JM (2007) Driven by the West Wind drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *J Biogeogr* 35:417–427
- Waters JM, Esa YB, Wallis GP (2001) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298
- Willig MR, Kaufman RM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Ann Rev Ecol Syst* 34:273–309
- Young MW (1929) Marine fauna of the Chatham Islands. *Trans Proc R Soc N Z* 60:136–166

Chapter 10

Pattern and Process in the Distributions and Biogeography of New Zealand Freshwater Fishes: The Diadromous Species

Abstract Diadromy is a dominating life history strategy in the fauna, with some diadromous species being widespread beyond New Zealand, reaching Australia and/or Patagonian South America. Some species are facultatively diadromous and can establish lacustrine populations. Some are found only in lowland locations, close to the sea, whereas others penetrate greater distances inland. The presence of falls and dams excludes some diadromous species, but a few are adept at climbing falls, and may be found long distances inland. Contemporary marine straits between the main islands of New Zealand do not influence the distributions of diadromous species, though some non-diadromous species have not been able to spread across these straits. However, some non-diadromous species are present on both sides of straits, probably as a consequence of land connections across straits at a time of lowered sea-levels in the Pleistocene.

Keywords Australia • Diadromy • Dispersal • Galaxiidae • Geographic ranges • Patagonian South America • Pleistocene • Sea level changes

A series of contrasts is drawn, above (Chapter 9), between diadromous and non-diadromous species with regard to patterns in diverse aspects of their distributions and ecologies. The challenge, now, is to explore synthesis of these patterns and their implications for historical and ecological biogeography. Again, some strong contrasts can, I believe (and at the most fundamental level), be attributed to whether or not species have regular marine (diadromous) stages in the life of each individual, and of each cohort. It applies at a hierarchy of spatial scales, and the dichotomy is very strong.

10.1 Diadromy as an Adaptive Life History Strategy

The presence of diadromy widely across all of the various families in the New Zealand freshwater fish fauna seems likely to be driven, at least in part, by its adaptive value. This value could accrue at several levels.

- (i) At the outset it is likely that diadromy has been functionally important in actually facilitating freshwater fish getting to a geographically isolated island archipelago like New Zealand in the first instance, i.e., the tolerance of marine salinities is likely to have been crucially important in allowing trans-oceanic dispersal to such an isolated land as New Zealand – such dispersals being earlier, historical manifestations of processes like the contemporary arrival of the Australian spotted eel in the past 25 years discussed earlier (Jellyman et al. 1996; McDowall et al. 1998d). Perhaps the persistence of diadromy, especially in the fish faunas of remote islands such as New Zealand, is a strategy that ensures that these islands' fresh waters are able to have their freshwater fish populations restored after local perturbations (McDowall 2009) and this was especially important if Zealandia disappeared entirely beneath sea in the Oligocene, as some suggest it did (Campbell and Hutching 2007; Landis et al. 2008).
- (ii) Diadromy also provided the basis for invasions of freshwater fish by species of marine ancestry (torrentfish and black flounder); it gave them access to freshwater habitats and they are able to return to sea for any phase of their life histories that they must for physiological reasons (something about which nothing is known).
- (iii) Diadromy is probably equally significant in allowing spread of the species around New Zealand and, as discussed elsewhere, in allowing recovery of fish faunas in streams following local extirpation caused by perturbation events, both short- and long-term (volcanism, land submergence and re-emergence, glaciation, river mouth closure – McDowall 1988, 1996a, b, 2000a), or when habitats become newly available.
- (iv) I have formerly suggested that diadromy may also be a mechanism that provided an escape for fishes from periods of low temperatures in freshwater ecosystems during the Pleistocene (McDowall 1970). Perhaps the sea was less challenging than freshwater habitats in winter; however, it seems certain that there were non-migratory freshwater fish species in New Zealand fresh waters throughout the same Pleistocene periods of climatic cooling, so that, for at least for some of them, these low temperatures did not fatally jeopardise survival, though they are almost certain to have retreated to lower elevations, at times of glacial advance, being driven out of the ice-filled valleys.
- (v) As well, when the impacts of temperature changes as a result of glaciation are viewed against the further backdrop of spawning season, it seems that in the galaxiids, at least, and thus for more than half the fauna, there could be two strategies that might have facilitated their survival through the Pleistocene. Spawning seasons of the diadromous galaxiid species are in late autumn and winter (McDowall 1990, 1995; McDowall and Kelly 1999; Allibone and Caskey 2000; Charteris et al. 2003). This means that galaxiid larvae are hatching and moving to sea as the coldest season approaches. Having larvae at sea may enable them to escape the severest cold temperatures in fresh water during the winter. Non-diadromous galaxiids, in contrast, spawn in late winter and spring, so that larval and early juvenile life takes place during the rising temperatures of spring and early summer (McDowall 1990, 2000b; Bonnett 1992b). The challenge for these

non-diadromous species may then be to grow sufficiently rapidly over the period from late spring, through summer and into autumn to allow the new year-class to go into the looming winter with enough body mass to survive through the period of lowest winter temperatures (Shuter and Post 1990). This may be particularly important for the species in the non-diadromous *Gl. vulgaris* complex species that are found in submontane streams of the Otago Peneplain of the southeastern South Island, and especially in upper reaches the Taieri River, though they, too, may have been driven to lower elevations at times of climatic cooling. Even though the extent of glacial advance across these Central Otago landscapes was not great, it would have been very cold there and streams would almost certainly have frozen in winter at higher elevations, as a few do even today.

10.2 Distributions of Diadromous Species at the Global Scale

Scope for oceanic dispersal in New Zealand's diadromous freshwater fish species is consistent with the very wide Southern Hemisphere-scale distribution patterns of some species, such as lamprey and inanga (McDowall 1988, 2002a), though they are not a key focus for the present study. Though few of New Zealand's diadromous species are found beyond the archipelago, the several that are known also from other, more distant, lands (variously, Australia, Patagonia, Falkland Islands) are all diadromous (lamprey, shortfin and spotted eel, inanga and koaro). No non-diadromous species in the New Zealand fauna is known elsewhere.

10.3 Why so Many Diadromous Species?

New Zealand has more diadromous species than almost any other comparable land area, and a greater proportion of diadromous species than any fish fauna of comparable or larger size (McDowall 1988, 1990). Diadromy is present in at least nine independent lineages in the fauna. This prompts the question "Why?" There are no unequivocal explicit answers, though we can speculate.

- (i) In part this high number of diadromous species may be because only diadromous species have been able to reach New Zealand's fresh waters since Zealandia became detached from Gondwana in the southwestern Pacific Ocean >80 million years ago, or since Zealandia emerged from complete inundation in the Oligocene, if Landis et al. (2008) are correct, i.e., that in substantial measure, there are fish here only because they are diadromous, and they brought their diadromy with them.
- (ii) Additional interesting aspects of the fauna are the very small number of species that are pool-dwelling, as well as a high degree of nocturnal behaviour and most species being highly cryptic, especially at night, for reasons that are not understood.

- (iii) But some diadromy almost certainly evolved here, and at least twice, in the torrentfish and black flounder, both of which probably have their closest affinities with fish species in New Zealand coastal seas, and diadromy may have provided access to freshwater habitats/niches that were unoccupied by other taxa.
- (iv) It may also, in part, be an outcome of New Zealand's turbulent geological history since it became detached from Gondwana, i.e. that diadromous species were pre-adapted to facilitating re-invasion of river systems as the geology and climate of New Zealand changed throughout the Cenozoic, whereas non-diadromous species would have suffered more local extirpation and have been less resilient under environmental stresses.

Scenarios discussed elsewhere in this book document how local and regional perturbations are likely to have caused local extirpations of freshwater fish faunas, and how it has been the diadromous species that have been best able to re-colonise the affected river systems. As we view these distributions, today, we are probably looking only at the most recent outcomes of continual, local-to-regional, perturbations, extirpations, redispersals, invasions, and reinvasions – up stream and down stream. The biotic impacts of a much longer history of these processes may well have been obscured or obliterated with the passage of time – similar processes of local extirpation and then recolonisation by diadromous species probably have taken place throughout New Zealand's geological history – what Brown and Kodric-Brown (1977) have labelled “the rescue effect”.

10.4 Ranges of Diadromous Fishes at the New Zealand-Wide Scale

As we have seen, diadromous species are generally very widespread in New Zealand's fresh waters. Apart from the localised presence of Stokell's smelt (Fig. 10.1 – □) and spotted eel, there is no within-New Zealand regional or local endemism among the diadromous species in the fauna. These species have the opportunity to disperse around New Zealand through the sea (and they clearly do so in a way that non-diadromous species do not and probably can't). There is little doubt that marine, coastal dispersal explains their wide ranges. Widespread latitudinal ranges of the diadromous species mean that they tend also to be widely sympatric at the site, catchment, and regional scales. Consistent with this is a lack of genetic structuring in populations across the ranges of such diadromous species (Barker and Lambert 1988; Allibone and Wallis 1993; Dijkstra and Jellyman 1999; Smith et al. 2001).

Several diadromous species in the New Zealand fauna are notably absent from the many rivers of the Canterbury Plains in the eastern South Island (though though they are widely present in western catchment at the same latitudes. There are, for instance, no records of shortjaw kokopu in the eastern/southern South Island from about Kaikoura south as far as western Southland (Fig. 10.2a – arrows). Banded kokopu is rarely present in the east apart from on Banks Peninsula (see Fig. 9.4e, arrow 1), as

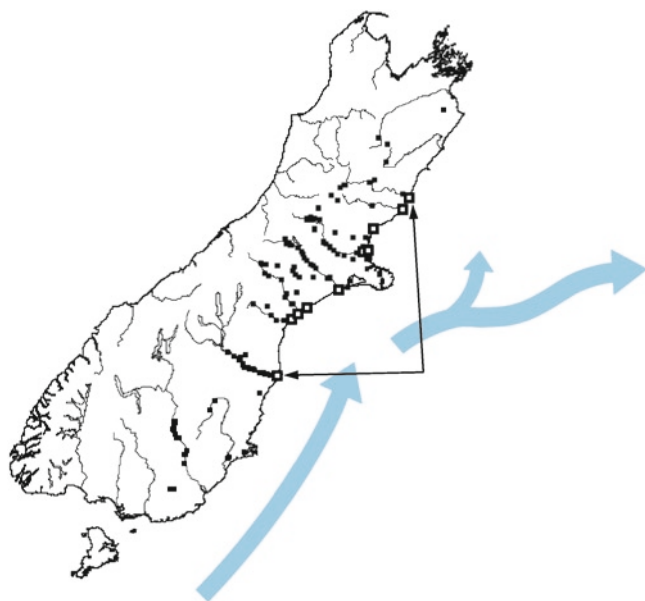


Fig. 10.1 Distributions of Stokell's smelt, *Stokellia anisodon* (■) and introduced Chinook salmon, *Oncorhynchus tshawytscha* (□), and ocean currents along east coast of South Island

are koaro (see Fig. 9.4d) and redfin bully (Fig. 10.2c). Giant kokopu is also very rare in this area. These patterns can be attributed substantially to lack of suitable habitats for these species in the unstable, shifting, gravelly braided rivers of the Canterbury Plains (Fig. 10.3) (Eldon 1989; McDowall 1990). But, other diadromous species are still widespread and abundant there, such as torrentfish (Fig. 10.2b) and bluegill bully, which abound in the braided gravelly rivers of the Canterbury Plains.

In addition, several of the species generally absent from the plains rivers systems are found primarily in small, stable streams, with coarse cobble/boulder substrates, often within forest – and these habitat conditions are seldom available in the rivers of the plains, and there is minimal indigenous forest left in the area. Some of these species, especially redfin bully (Fig. 10.2c), do turn up in the more stable, often forested, boulder-cobble streams along the Kaikoura coast of the northeastern South Island, and also on Banks Peninsula which appear to comprise a 'habitat island' among the many more unstable gravel-bedded, braided rivers of the Canterbury Plains. It is no coincidence that the areas where these species are found are also the areas where there is hilly landscape close to the sea coast.

Human habitat degradation has also undoubtedly contributed to absence of some of these species – especially deforestation and the drainage of the formerly vast wetlands of the Canterbury Plains (Andersen 1916; Dobson 1930; Acland 1951; Graham and Chapple 1965; McGlone 1983; McDowall 1998). Giant kokopu, at least, were once probably much more widespread there (Studholme 1940); and yet, apart from a landlocked population in Horseshoe Lagoon, a small coastal wetland south of Timaru,

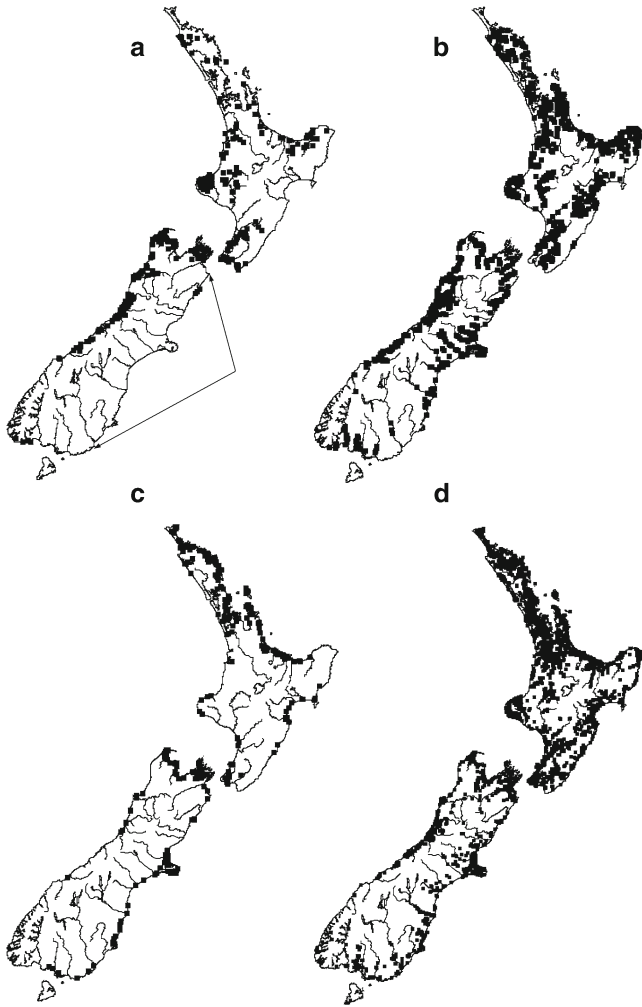


Fig. 10.2 Distributions of: **a.** shortjaw kokopu, *Galaxias postvectis*. **Arrows** - ↑1: absence along eastern coastlines of South Island); **b.** torrentfish, *Cheimarrichthys fosteri*; **c.** redfin bully, *Gobiomorphus huttoni*; **d.** bluegill bully, *Gb. hubbsi*

there has, as far as I know, been only one record of giant kokopu between Kaikoura and Dunedin in the past 50 years. Apart from the habitat suitability/habitat loss issue, there may also be a recruitment issues for some diadromous species. It is possible that, with insufficient progeny reaching the coastal seas of the eastern South Island from which to invade the rivers there (David et al. 2004), these rivers are ecological/recruitment “sinks” with recruitment rates being below the threshold to enable establishment of “source” (self-recruiting) populations (Pulliam 1988).

Several additional areas have impoverished communities of diadromous fishes. Fiordland, in far southwestern New Zealand, is one such area that has nearly virgin

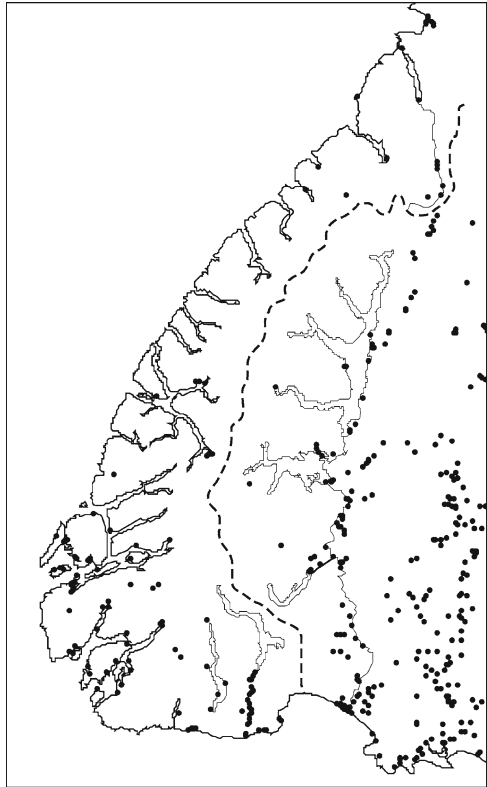


Fig. 10.3 The Rakaia River, one of the large, shifting, braided rivers of the Canterbury Plains

indigenous forest, but where observed sparseness of fish (low species richness as well as low individual abundance) seems not to be due altogether to inadequate sampling in that area. Although, compared with more easily accessible areas of New Zealand, there are relatively few fish faunal sampling sites in Fiordland (southwestern South Island), there have been several focused surveys of freshwater fishes there (NZFFD records >180 sites from the streams of western and southern coastal Fiordland: McDowall 1981; Bonnett and James 1988; McDowall and Sykes 1996 – see Fig. 10.4). In those areas of Fiordland that have been well sampled, the fauna has been found to be distinctly impoverished. Species, that are widely present a little further north in the rivers of South Westland, or in rivers to the east and south across Southland (Waiau – McDowall 1994a; Wairaurahiri – McDowall and Sykes 1996; Oreti and Mataura – McDowall and Lambert 1996) – such as common smelt, shortjaw kokopu (Fig. 10.2a), giant kokopu, torrentfish (Fig. 10.2b), giant bully (Fig. 10.2c) and shortfin eel have not been found, or were found only occasionally, in Fiordland rivers, though redfin bully, banded kokopu, koaro, inanga and longfin eels were found to be widely present there.

Causes for this biotic impoverishment in Fiordland streams are undiscovered, and this is a question that needs detailed ecological study. It may result partly from the extremely heavy rainfall along the Fiordland coast (up to 12,000 mm of rain per year: Griffiths and McSaveney 1983) – which may create severely and repeatedly disturbed habitats in Fiordland rivers and streams, making them inhospitable to long-term occupation by some fish species – the topography is also very steep, the combination of heavy rainfall and steepness making for frequent major flood events. There may also be juvenile recruitment difficulties in Fiordland rivers – patterns of oceanic circulation in the vicinity may create difficulties for the small juveniles of some diadromous species as they seek to return to freshwaters from the sea. The strong oceanic currents that sweep eastwards through Foveaux Strait

Fig. 10.4 NZFFD sampling sites in Fiordland, in the southwestern South Island (dotted line approximates the western/eastern catchment boundaries)



between the southern tip of the South Island and Stewart Island (Carter 2001), may restrict juvenile recruitment into these southern rivers, but the absence or rarity of certain species begs the question of why others seem to be able to recruit there from the sea, and are more common and widespread. Their high general abundance may be the key, through providing higher propagule pressure.

Similar distribution/recruitment issues may apply to the fish fauna of Stewart Island (Chadderton and Allibone 2000). Shortjaw kokopu (Fig. 10.2a) and torrent-fish (Fig. 10.2b), for instance, have never been recorded there, and it may be no coincidence that these are much the same species as are absent from western Fiordland, and also from the Chatham Islands.

10.5 Two Diadromous Species with Narrow Latitudinal Range

In contrast with the generality that diadromous species usually have much wider ranges are some distinctive distributions that are inconsistent with the general patterns and/or enigmatic absences of diadromous species from certain areas.

A highly idiosyncratic distribution of a diadromous species is the restricted range of Stokell's smelt (Fig. 10.1 – large open squares □). This species is present only along the Canterbury coastline in the eastern South Island, and in only the larger rivers such as the Waimakariri, Rakaia, Ashburton, Rangitata and Waitaki. It is not recorded from the many smaller rivers there, such as the Waipara, Ashley, Hinds, Orari, Opihi, Waihao, Pareora, Otaio, Makihikihi, and others. This is an intriguing absence that may be a habitat suitability issue in these rivers, though the absence of Stokell's smelt could be due partly to these small rivers often having blocked outlets to the sea during summer as a result of low flows – this happening at the time when Stokell's smelt is invading lowland rivers from the sea, and is present in vast numbers in the larger, lowland rivers of Canterbury (Davis et al. 1983; Bonnett 1992a) – depending on timing, mouth blockage will either inhibit the entry of adult spawners from coastal seas, or affects the exit to sea of the newly hatched larvae deriving from any adults that do achieve access to the smaller rivers – there may have been historic selective adaptation to only entering those rivers that were reliably open, enabling migrations to and from the sea, and these would have tended to be the larger, shingly braided rivers.

No obvious explanation for the narrow range of Stokell's smelt has been suggested, though it may have something to do with ocean currents along the Catlins coastline. The Southland Current flows in a north-easterly direction near the east coast of the South Island (see Fig. 10.1 – small filled squares – ■; Carter 2001), after sweeping from the Tasman Sea to the west of New Zealand, around the southern tip of the South Island, and then north to north-east off the South Island's east coast, gradually diverging eastwards, from land, into the southwestern Pacific Ocean across the Chatham Rise. In so doing, this current system encloses an elongated, roughly triangular, parcel of sea into which the few rivers, where Stokell's smelt is known, flow. Perhaps the current systems constrain the range of this fish. Interestingly, there are stocks of Chinook salmon (*Oncorhynchus tshawytscha* – f. Salmonidae) which were introduced into New Zealand from North America in the early 1900s (McDowall 1994b – and which long represented the only confirmed, globally-long-term, successful, translocated stocks of any Pacific salmon species anywhere in the world (but see Pascual et al. 2001; Becker et al. 2007). They have a somewhat broader though superficially similar distribution along the east coast of the South Island (McDowall 1990; Bonnett 1992a: Fig. 10.1). Thus, these oceanic currents may provide an offshore boundary within which both Stokell's smelt and Chinook salmon are distributed. The similarities in their distributions may imply common explanations, though this, too, does beg the question of why similar range limitations do not apply also to the many other diadromous fishes present and often abundant in the rivers of the eastern South Island (such as lamprey, two species of eel, common smelt, inanga, koaro, torrentfish, giant, common, and bluegill bullies and black flounder).

The spotted eel has limited and intermittent New Zealand range. It appears to have begun arriving in there only in the last third of the twentieth century (though this could be a second spasm of arrival – Phillipps 1925). Otherwise, it was not recognised there until the mid-1990s (Jellyman et al. 1996; McDowall et al. 1998).

Its New Zealand distribution is not nearly as well documented as the distributions of other indigenous fish species, partly owing, perhaps, to the species' recent arrival and recent recognition. There are also difficulties in its identification, especially when small, when it is indistinguishable from similar sized New Zealand longfin eels – and many individuals of spotted eel will necessarily be small as a consequence of this species' relatively recent arrival in New Zealand rivers. And, as noted earlier, it is possible that its arrival is episodic and related to some unidentified fluctuating patterns in the oceanic circulation in the tropics and sub-tropics to the north and west of New Zealand. There have been suggestions that recruitment of other eel species to New Zealand may also be episodic, and there may be undiscovered patterns of fluctuating arrival of new cohorts of all of these eels that relate to periodic changes in the patterns of ocean current systems in the western subtropical and southern Pacific Ocean: nothing is known.

10.6 Facultativeness in Abandoning Diadromy

Across the diversity of diadromous species present in New Zealand fresh waters, there is considerable variation in various species' capacity to abandon diadromy and spend their whole lives in fresh water, though in some groups, it seems that diadromy is obligatory.

- (i) There are, for example, no non-diadromous populations of the local diadromous lamprey species (though some other lamprey genera, elsewhere, are facultatively diadromous, both in Australia and around the Northern Hemisphere at boreal latitudes, implying that diadromy is not a physiological imperative for lampreys, more generally: Hubbs and Potter 1986; McDowall 1988).
- (ii) Nor do any of New Zealand's freshwater eels establish non-diadromous populations, and that is true of all anguillid eels, globally (Tesch 2003) – it is as if reproduction and/or larval life at sea are physiological imperatives for anguillid eels though, as discussed elsewhere, there is growing evidence that anguillids may sometimes abandon entry into fresh water and spend their entire lives at sea, perhaps in areas of lowered salinity (Tsukamoto et al. 1998; Tsukamoto and Arai 2001; McCleave and Edeline 2009); this has no significant implications for freshwater fish communities.
- (iii) Nor was there any evidence that New Zealand's now extinct *Prototroctes* grayling ever established landlocked populations (and neither can its Australian sister species apparently do so – McDowall 1996c). Hector (1872) wrote of his belief that “the very large fish locally called a trout, which are sometimes cast up on the beaches of the great inland lakes of Otago, also belong to this species [i.e. the grayling]. These probably reach 6 or 8 lbs. in weight”. Hector's account is a total enigma and nothing known of the fauna today permits us to unequivocally identify the fish he was writing about. No other suggestions of lake populations of this species are present in the early New Zealand literature, nor was

the grayling ever reliably reported as growing to “6 or 8 lbs”, the largest being only a fraction of that size. Thus, what else is known of the grayling bears little similarity to Hector’s account, and we cannot discount the possibility that what he wrote was based entirely on hearsay.

- (iv) Common smelt easily establishes lake-limited populations (see Fig. 18.3a, but Stokell’s smelt is never known to do so.
- (v) Among the five New Zealand diadromous galaxiids, there are numerous lake-limited populations of koaro (see Fig. 18.3b), a few of banded kokopu and giant kokopu, occasional instances of inanga in New Zealand (but plenty of them in Australia, Patagonia and the Falkland Islands – McDowall 1972; McDowall et al. 2001); and there are no lake-limited populations of shortjaw kokopu. Smaller numbers of lacustrine stocks of inanga, banded and giant kokopu may reflect the smaller number of suitable and accessible lakes.
- (vi) There is similar intrageneric variability in the diadromous *Gobiomorphus* bullies, amongst which common bully has established many lake populations though giant, redfin and bluegill bullies have apparently never done so.
- (vii) And, as noted earlier, two diadromous New Zealand freshwater fishes (torrent-fish and black flounder) seem to have an ancestry among local marine fish species, and neither of these has established non-diadromous stocks and they seem to be locked into spending part of their life cycles at sea.

The extent to which this variation in life history flexibility, or facultativeness, has:

- (i) Ancestral/phylogenetic roots
- (ii) Is driven by physiological imperatives, and/or
- (iii) Is driven by issues of habitat suitability/availability

is unclear. There is no obvious reason why more than one of these influences may not have been, together, significant, either across the diadromous fauna as a whole, or within individual species. What is certain is that facultativeness is highly variable, and that where species can be flexible, this opens up additional opportunities for occupying habitats that would otherwise be inaccessible or inhospitable, and it also provides opportunities for the eventual evolution of non-diadromous derivative species in the geographical isolation offered by lakes, as with dune lakes galaxias (derived probably from inanga: See Chapter 13; and McDowall 1970, 1972) and Tarndale bully (derived from common bully: McDowall and Stevens 2007; Stevens and Hicks 2009: see Chapter 15).

The koaro, especially, has widely invaded many of the submontane lakes that formed after retreat of Pleistocene glacial ice (see Fig. 18.3b), and it has reached some lakes that would seem to defy invasion by a fish migrating up stream, such as Boulder Lake in the mountains inland from Nelson, which drains via a fall c. 60 m high. It is also present in many other high elevation lakes and tarns, some without existing outlets. Other species have also often become established in inland lakes, especially common smelt (see Fig. 18.3a) and common bully. It should be noted, however, that some reported populations of both common smelt and common bully are known, or are believed, to have established lake populations as a result of

human translocation, either by Polynesian Maori prior to European settlement, or by trout fisheries managers since European settlement in the mid-1800s. This history is poorly documented in detail and much of the knowledge is anecdotal. Various of the above species have found their way into the volcanic lakes of the central/northeastern North Island, where Maori translocation seems almost certain (McDowall 1972, 1990, 1994c, *in press*; Strickland 1993), and this is possibly true also, for instance, of a smelt population in a small sub-alpine tarn near Lake Ohau (see Fig. 18.3a, arrow 4), or it was possibly stocked by trout fisheries managers (Elkington and Charteris 2005).

It is possible that some of the translocations were inadvertent, with additional fish species being unwittingly shifted among the intended species (sometimes perhaps common bully with trout, or perhaps when common smelt were being shifted from the Waikato River into trout lakes in the central North Island; McDowall 1994c). The likelihood of this happening to common smelt is reduced, rather, by its great fragility and vulnerability to handling, though clearly some past human translocations have been effective, especially into lakes of the central North Island, though not exclusively there. Lake populations of common smelt in other parts of the country, as in Lakes Poerua and Brunner in the Grey River catchment in Westland, also have anthropogenic origins (McDowall 2002b), as is also true of populations in Lake Opouahi, in Hawkes Bay, and the Putere Lakes inland from Gisborne (McDowall 1990).

10.7 Upstream Penetration and the Effects of Falls and Dams on the Ranges of Diadromous Species

A corollary of all the ‘advantages’ discussed above for diadromous species, associated with their dispersal around the New Zealand coastline and their opportunities to invade rivers from the sea, is that they are likely to exhibit limited upstream penetration. Distinctions among the diadromous species in how far upstream they move (see sections 9.8 and 9.10) and the elevations they attain are, at least in part, a product of the combination of:

- (i) Each species’ upstream instinctive migratory ‘drive’
- (ii) Its ability to swim or climb upstream past swift rapids, torrents or even falls
- (iii) The gradient characteristics of the rivers themselves, either their overall gradients or the presence of river reaches with swift rapids, torrents or falls

There is an informal continuum. Species like Stokell’s smelt (Figs. 9.7c, 10.1) common smelt (see Fig. 18.3a), inanga (Fig. 9.7e), and giant bully (see Fig. 10.2c) seldom penetrate far beyond the estuaries and, where the penetration is greatest, it is primarily when river gradients are very shallow. Other species may move upstream very long distances, even in rivers with steep gradients, involving species like lamprey (Fig. 9.4a – 230 km inland), longfin eel (Figs. 9.4b, 9.7a – 314 km), shortfin eel (Figs. 9.4c, 9.7b – 292 km), koaro (Figs. 9.4d, 9.7f – 400 km), banded kokopu (Fig. 9.4e – 177 km) and shortjaw kokopu (Fig. 9.7d – 206 km). Some are capable

of climbing vertical falls 10s of metres high. Others, of course, which have intermediate climbing ability, such as redfin bully, exhibit intermediate inland penetration. An outcome of these differences in upstream penetration is that there are extensive areas of inland habitat that appear proximally well-suited to various of the diadromous species, but where some or all of them are not found owing, it seems, to the difficulties of cohort-scale upstream access from the sea, via river mouths.

10.8 Implications for the Distributions of Diadromous Fishes of the Marine Straits Between the Main Islands of New Zealand

The North and South Islands of New Zealand are separated by Cook Strait, a seaway about 23 km wide; similarly South and Stewart Islands are separated by Foveaux Strait, which is about 26 km wide (see Fig. 2.1). The distributions of all diadromous species other than Stokell's smelt span Cook Strait, basically as though it was not there (see Figs. 9.4, 10.2), and the strait has clearly not constituted a significant barrier to their spread. Many diadromous species are similarly present on both sides of Foveaux Strait, though some are not on Stewart Island (for various reasons discussed earlier). Their absence there is probably not due to the presence of the sea strait itself, though the swift tidal currents through Foveaux Strait may influence what species are present on Stewart Island.

10.9 Occupation of the Aupouri Peninsula in Northern New Zealand

The far northern tip of the North Island of New Zealand (see Fig. 3.3) was formerly a small island that was well separated from what was ancestral, northern North Island – which then extended northwards only to about Kaitia. Land connection was established by formation of a northward extending sand tombolo during the Pleistocene (Brook 1999). There is no hint that the distributions of any diadromous species reflect former existence of this ocean gap – as would be expected from the responses of diadromous species to other perturbations and landform changes.

References

- Acland J (1951) The early Canterbury runs. Whitcombe & Tombs, Christchurch, N Z, 427 pp
- Allibone RM, Caskey D (2000) Timing and habitat of koaro (*Galaxias brevipinnis*) spawning in streams draining Mt Taranaki, New Zealand. N Z J Mar Freshwater Res 34:593–595
- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). Biol J Linn Soc 50:19–33

- Andersen JC (1916) Jubilee history of South Canterbury. Whitcombe and Tombs, Wellington, N Z, 775 pp
- Barker JR, Lambert DM (1988) A genetic analysis of populations of *Galaxias maculatus* from the Bay of Plenty: implications for natal river return. N Z J Mar Freshwater Res 22:321–326
- Becker LA, Pascual M, Basson NG (2007) Colonization of southern Patagonia ocean by exotic Chinook salmon. Conserv Biol 21:1347–1352
- Bonnett ML (1992a) Distribution and freshwater residence of Stokell's smelt, *Stokellia anisodon* (Stokell), in the South Island, New Zealand. N Z J Mar Freshwater Res 26:213–218
- Bonnett ML (1992b) Spawning in sympatric alpine galaxias (*Galaxias paucispondylus* Stokell) and longjawed galaxias (*G. prognathus* Stokell) in a South Island, New Zealand high-country stream. N Z Nat Sci 19:27–30
- Bonnett ML, James GD (1988) Freshwater fish in preservation and chalky inlets. Freshwater Catch (N Z) 34:12–14
- Brook FJ (1999) Stratigraphy and landsnail faunas of Late Holocene dunes, Tokerau Beach, northern New Zealand. J R Soc N Z 29:337–359
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Carter L (2001) Currents of change: the ocean flow in a changing world. Water Atmos 9(4):15–17
- Chadderton WL, Allibone RM (2000) Habitat use and longitudinal distribution patterns of native fish in a near Stewart Island, New Zealand stream. N Z J Mar Freshwater Res 34:487–499
- Charteris SC, Allibone RM, Death RG (2003) Spawning site selection, egg development, and larval drift of *Galaxias postvectis* and *G. fasciatus* in a New Zealand stream. N Z J Mar Freshwater Res 37:493–506
- David B, Chadderton L, Closs G, Barry B, Markwitz A (2004) Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*). DOC Sci Int Ser 160:1–23
- Davis SF, Eldon GA, Glova GJ, Sagar PM (1983) Fish populations of the lower Rakaia River. N Z Min Agric Fish Fish Environ Rep 33:1–109
- Dijkstra LH, Jellyman DJ (1999) Is the subspecies classification of the freshwater eels *Anguilla australis australis* Richardson and *A. australis schmidtii* Phillipps still valid? Mar Freshwater Res 50:261–263
- Dobson AD (1930) Reminiscences of Arthur Dudley Dobson, engineer, 1841–1930. Whitcombe and Tombs, Auckland, N Z, 225 pp
- Eldon GA (1989) Whither the Banks Peninsula redfin. Freshwater Catch (N Z) 39:12–13
- Elkington SP, Charteris SC (2005) Freshwater fish of the upper Waitaki River. Department of Conservation, Christchurch, N Z, 44 pp
- Graham GW, Chapple LJB (1965) Ellesmere County: the land, the lake, and the people. Ellesmere County Council, Christchurch, N Z, 221 pp
- Griffiths GA, McSaveney MJ (1983) Hydrology of a basin with extreme rainfall: Cropp River, New Zealand. N Z J Sci 26:293–306
- Hector J (1872) Notes on the edible fishes of New Zealand. In: Hutton FW, Hector J (eds) fishes of New Zealand. Government Printer, Wellington, N Z, pp 95–133
- Hubbs CL, Potter IC (1986) Distribution, phylogeny and taxonomy. In: Hardisty MW, Potter IC (eds) The biology of lampreys. Academic, London, pp 1–65
- Jellyman DJ, Chisnall BL, Dijkstra LH, Boubée JAT (1996) First record of the Australian long-finned eel, *Anguilla reinhardtii*, in New Zealand. Mar Freshwater Res 47:1037–1040
- Landis C, Campbell HJ, Begg JG, Mildenhall DC, Paterson AS, Treweek SA (2008) The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. Geol Mag 145:173–197
- McCleave JD, Edeline E (2009) Diadromy as a conditional strategy: patterns and drivers of eel movements in continental habitats. Amer Fish Soc Symp 69:97–120

- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). *J R Soc N Z* 2:325–367
- McDowall RM (1981) Freshwater fish in Fiordland National Park. *N Z Min Agric Fish Fish Environ Rep* 12:1–31
- McDowall RM (1988) Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London, 309 pp
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1994a) Native fish populations of the Waiau River (Southland) and the impacts of the Lake Manapouri control structure (the Mararoa Weir). NIWA Consul Rep SRC005:1–58
- McDowall RM (1994b) The origins of New Zealand's Chinook salmon, *Oncorhynchus tshawytscha*. *Mar Fish Rev* 56:1–7
- McDowall RM (1994c) Gamekeepers for the nation: the story of New Zealand's acclimatisation societies, 1861–1990. Canterbury University Press, Christchurch, N Z, 512 pp
- McDowall RM (1995) Seasonal pulses in migrations of New Zealand diadromous fish and the potential impacts of river mouth closure. *N Z J Mar Freshwater Res* 29:517–526
- McDowall RM (1996a) Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Can J Fish Aquat Sci* 53(Suppl 1):219–236
- McDowall RM (1996b) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1996c) Family Prototroctidae – southern graylings. In: McDowall RM (ed) Freshwater fishes of southeastern Australia. Reed, Chatswood, NSW, pp 96–98
- McDowall RM (1998) Once were wetlands. *Fish Game N Z* 20:31–39
- McDowall RM (2000a) Biogeography of the New Zealand torrentfish *Cheimarrichthys fosteri* (Teleostei: Pinguipedidae): a distribution driven mostly by ecology and behaviour. *Environ Biol Fishes* 58:119–131
- McDowall RM (2000b) Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 224 pp
- McDowall RM (2002a) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2002b) Like a thief in the night. *Fish Game N Z* 37:34–36
- McDowall RM (2009) Why be amphidromous: expatrial dispersal and the place of source and sink dynamics. *Rev Fish Biol Fisher* doi. doi:10.1007/s11160-009-9725-2
- McDowall RM (in press) Ikawai: freshwater fishes in Maori culture and economy. Canterbury University Press, Christchurch, New Zealand
- McDowall RM, Kelly GR (1999) Date and age at migration in juvenile giant kokopu, *Galaxias argenteus* (Gmelin) (Teleostei: Galaxiidae) and estimation of spawning season. *N Z J Mar Freshwater Res* 33:263–270
- McDowall RM, Lambert P (1996) Fish and fisheries values of the lower Maitai River: an assessment of values and implications of effluent discharges to the river. NIWA Consult Rep COO605/1:1–17
- McDowall RM, Stevens MI (2007) Taxonomic status of the Tarndale bully, *Gobiomorphus alpinus* (Teleostei: Eleotridae) revisited, again. *J Roy Soc N Z* 37:15–29
- McDowall RM, Sykes JRE (1996) Fish survey of the Wairaurahiri River, western Southland. NIWA Consult Rep SRC005/2:1–35
- McDowall RM, Jellyman DJ, Dijkstra LH (1998) Arrival of an Australian anguillid eel in New Zealand: an example of transoceanic dispersal. *Environ Biol Fish* 51:1–6
- McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands freshwater fishes. *Aquatic Conserv: Mar Freshwater Ecosyst* 11: 473–486
- McGlone MS (1983) Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeol Oceania* 18:11–25

- Pascual M, Bentzen P, Rossi CR, Mackey G, Kinnison MT, Walker R (2001) First documented case of anadromy in a population of introduced rainbow trout in Argentina. *Trans Am Fish Soc* 130:56–67
- Phillipps WJ (1925) New Zealand eels. *N Z J Sci Tech* 8:28–30
- Pulliam HR (1988) Sources, sinks and population regulation. *Am Nat* 43:187–193
- Shuter B, Post J (1990) Climate, population viability, and the zoogeography of temperate fishes. *Trans Am Fish Soc* 119:314–336
- Smith PJ, Benson PG, Stanger C, Chisnall BJ, Jellyman DJ (2001) Genetic structure of New Zealand eels *Anguilla dieffenbachii* and *A. australis*. *Ecol. Freshwat Fish* 10:132–137
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Strickland RR (1993) Pre-European transfer of smelt in the Rotorua-Taupo area, New Zealand. *J R Soc N Z* 23:13–28
- Studholme EC (1940) Te Waimate: early station life in New Zealand. Reed, Dunedin, N Z, 296 pp
- Tesch FW (2003) The eel. Blackwell, Oxford, 408 pp
- Tsukamoto K, Arai T (2001) Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habits. *Mar Ecol Prog Ser* 220:265–276
- Tsukamoto K, Nakae I, Tesch WV (1998) Do all freshwater eels migrate? *Nature* 396:635

Chapter 11

Pattern and Process in the Distributions of Non-diadromous Species – 1:

The *Galaxias vulgaris* Species Complex

Abstract The non-diadromous *Galaxias vulgaris* species complex, comprising about 10 genetic lineages, is confined to South and Stewart Islands, primarily to the east of the Southern Alps, though there are a few populations to the northwest of the northern Southern Alps. They fall into two morphotypes, informally called ‘flatheads’ (6 lineages) and ‘roundheads’ (4 lineages). Species richness is low in the north and greatest in the southern sector of the South Island. Greatest diversity in the south, is on an area that is regarded by some as a residual emergent island during the Oligocene marine submergence of much of New Zealand, where 8 of the lineages are found. Distributions of lineages overlap broadly in the south, though sympatry of lineages is only occasional, and where there is sympatry there is minimal evidence for hybridisation. Patterns of distribution tend to connect strongly to existing river catchments, though there are interesting instances where apparently anomalous occurrences relate to known changes in riverine connections associated with changes in earth history and topography.

Keywords Distribution • Earth history • Flathead galaxiids • *Galaxias vulgaris* • Galaxiidae • Roundhead galaxiids • Southern Alps

11.1 General Pattern in the Non-diadromous Species

Because of differences in dispersibility, and in particular the consequential inability to spread around coastal seas, non-diadromous species exhibit distinctive patterns of distribution compared with those of diadromous species. As was discussed earlier, geographical ranges of non-diadromous species are much narrower. Thus, in the following several chapters I address for non-diadromous species in the fauna, issues relating to their ecological and biogeographical history. An understanding of phylogenetic relationships within monophyletic species groups becomes crucial to informed interpretation of pattern, as the non-diadromous species groups exhibit a much greater tendency to have allopatric distributions in a way that is not true of diadromous species, which are generally broadly sympatric.

These chapters build on the brief synopses of the families in Chapter 7.

Non diadromous species are present only in the families Galaxiidae (21 of the 26 species or lineages – Table 1.1) and Eleotridae (three of the seven species) (McDowall 1990, 2000; McDowall and Stevens 2007; Stevens and Hicks 2009). Thus, this chapter, and some of those that follow (Chapters 12–15), deal only with these families. Enough is known about the phylogenetic relationships of some of these taxa to provide quite well-authenticated species groups, as follows (references are given in the relevant detailed sections): In these families there are:

- (i) The group of species, referred to as the *Galaxias vulgaris* species complex (Fig. 11.1), that is widespread in the eastern and southern South Island and Stewart Island (Figs. 11.2 and 11.3) (McDowall and Wallis 1996; McDowall 1997b; McDowall and Chadderton 1999), is dealt with in the present chapter.
- (ii) Five species of *Galaxias* are referred to by McDowall and Waters (2003), and here, as the ‘pencil-galaxias’ on account of their elongate, slender form (see Figs. 1.8 and 12.1): this species group is widespread from the eastern/central North Island south to inland Southland, and is covered in Chapter 12 (see Figs. 12.2–12.4).
- (iii) The dune lakes galaxias (see Fig. 13.1) is a species that is regarded as a land-locked derivative of the diadromous inanga (McDowall 1970; Ling et al. 2001), and which is present in a series of small lakes on the north head of the Kaipara Harbour, and in the Kai Iwi Lakes, a little north of Dargaville, discussed in Chapter 13 (see Fig. 13.2).
- (iv) The five species of mudfish (genus *Neochanna* – see Figs. 1.5 and 14.1), which form a monophyletic group in New Zealand, these together being a sister group of the diadromous Australian mudfish, *N. cleaveri* (McDowall 1997a; Waters and McDowall 2005): these species are widespread from far northern Northland, south as far as the Waitaki River valley in the eastern/central South Island and are discussed in Chapter 14 (see Fig. 14.3, arrow 9).
- (v) The three species of non-diadromous bullies (genus *Gobiomorphus* – see Figs. 1.6, 1.7, and 15.1) (Stevens and Hicks 2009), which are dealt with in Chapter 15.

11.2 Phylogenetic Relationships, Distributions and Biogeography in the *Galaxias vulgaris* Species Group

The *Gl. vulgaris* species group comprises about 10 non-diadromous lineages that are recognised substantially from studies of mtDNA, and which are present primarily in the eastern South Island and on Stewart Island (Figs. 11.2 and 11.3). Six specific names have been applied to these lineages and the other four lineages are not formally described; postulated relationships, based on molecular data (mtDNA) are shown in Fig. 7.7 (adapted from Waters and Wallis 2001a); however, data from

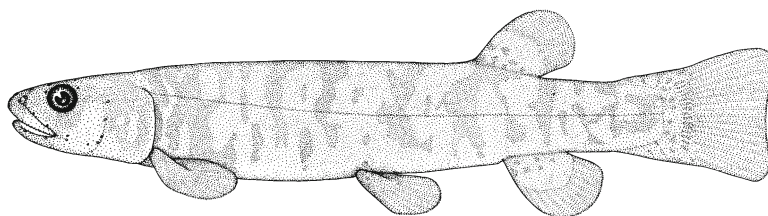


Fig. 11.1 Canterbury galaxias, *Galaxias vulgaris*, 100 mm LCF (family Galaxiidae)

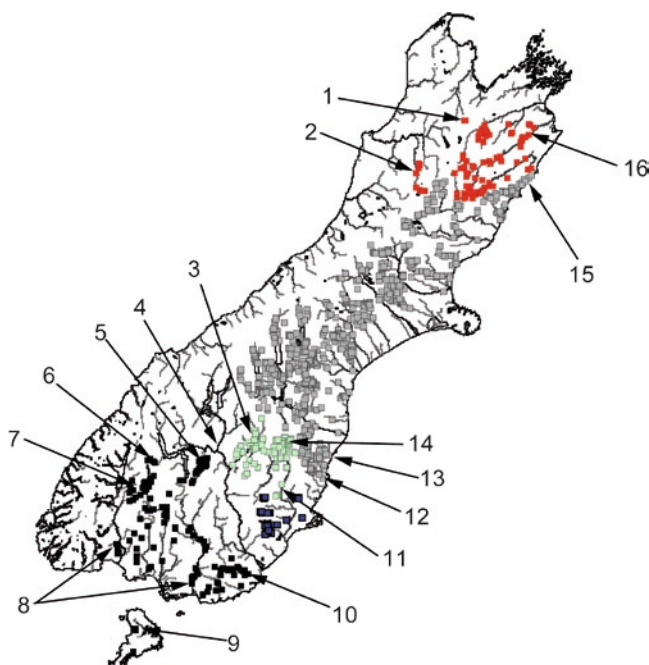


Fig. 11.2 Distributions of some of the lineages in the *Galaxias vulgaris* complex: *Galaxias* 'northern' (■); Canterbury galaxias, *Gl. vulgaris* (■), Central Otago roundhead galaxias, *Gl. anomalus* (■), Eldon's galaxias, *G. eldoni* (■) Gollum galaxias – *G. gollumoides* (■) (see also figure 11.3). **Arrows** – ↑1: Motueka River; ↑2: headwaters of the Maruia River, west-flowing Buller River system; ↑3: Manuherikia River, Clutha River system and upper Taieri River; ↑4: absence from the Kawarau River; ↑5: Nevis River, tributary of the Kawarau River; ↑6: Von River; ↑7: western limits for species complex in the Waiau River system western Southland; ↑8: widespread across Southland Plains; ↑9: Stewart Island southern limits of Canterbury galaxias at Waitaki River; ↑10: streams in the Catlins; ↑11: downstream limits near town of Middlesmarch in the mid Taieri valley; ↑12 & 13: lineages in Kakanui, Shag and Waianakarua Rivers on the coast south of the Waitaki River of uncertain identity and relationships; arrow ↑14: upper reaches of the Taieri River; ↑15: northern limits of Canterbury galaxias along the Kaikoura coastline north of the Conway River; ↑16: populations in north flowing Wairau River

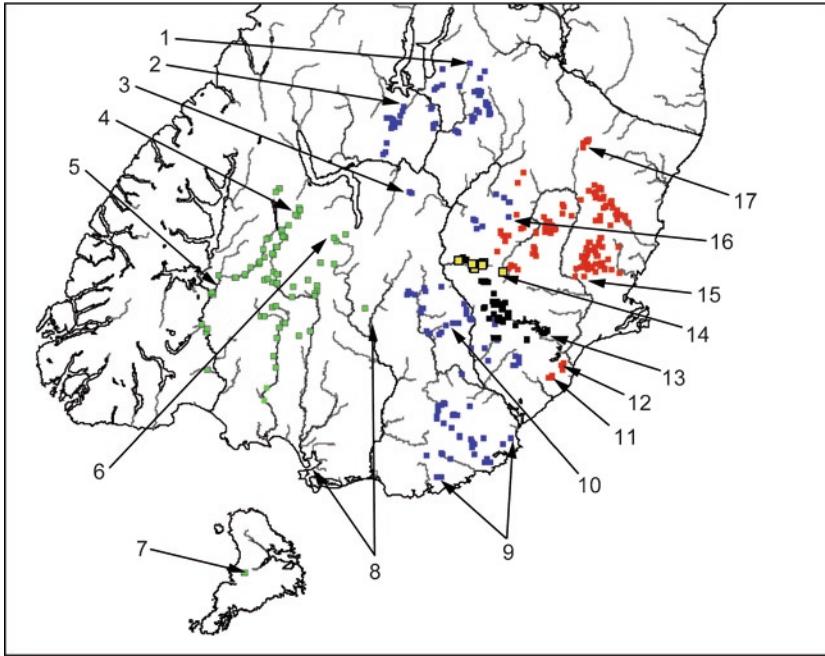


Fig. 11.3 Distributions of additional lineages in the *Galaxias vulgaris* species complex: Clutha flathead galaxias, *Galaxias* 'species D' (■), Taieri flathead galaxias, *G. depressiceps* (■), dusky galaxias, *G. pullus* (■), Southland flathead galaxias, *Galaxias* 'southern' (■), *Galaxias* 'teviot' (■). **Arrows** – ↑1: Lindis River, in headwaters of Clutha River system; Kyeburn River, northern headwaters of the Taieri River system; ↑2: Cardrona River, Clutha River system; ↑3: Bannock Burn, near confluence of Clutha and Kawarau Rivers; ↑4: Von River, a Lake Wakatipu tributary, Clutha River system; ↑5: Excelsior Creek, Waiau River system; ↑6: Bushy Creek, upper Maitara River; ↑7: Stewart Island; ↑8: lower Maitara River; ↑9: Catlins river systems; ↑10: lower-mid Clutha River; ↑11: Waipori River; ↑12: Narrowdale, tributary of the Tokomairiro River; ↑13: Akatore Stream, an independent coastal catchment south of the Taieri River; ↑14: Red Swamp Creek, headwaters of the Taieri River; ↑15: downstream limits of flathead galaxias in the vicinity of Middlemarch; ↑16: Maori Creek, upper Manuherikia River; ↑17: Kye Burn, upper Taieri River

nuclear gene DNA sequences are pointing to some alternative patterns of relationships (Waters *et al.* submitted), so that the lineages and taxonomy are perhaps a little less clear than originally thought. Part of the diversity in this species complex could relate to the former presence of one large lake or a series of lakes, in Central Otago, in Miocene times, c. 12–8 million years ago (Palaeolake[s] Manuherikia). Douglas (1986) and Lee and Forsyth (2008) described lakes as large as 5,600 km², and some of the diversification in the *Gl. vulgaris* species complex could have taken place in tributaries associated with these lakes, though we will probably never know. Certainly, there were galaxiids of this general type in the area in the Miocene, up to about 20 million years ago (McDowall 1976; McDowall and Pole 1997; Lee *et al.* 2007).

A substantial series of molecular and morphological studies over the past decade has been slowly unravelling the identity and relationships among these lineages, and is revealing complex taxonomic diversity (the taxonomy is still fluid and the number of lineages that will be formally recognised is yet to be decided – but see Allibone and Wallis 1993; Allibone et al 1996; McDowall 1997a; McDowall and Wallis 1996; King and Wallis 1998; McDowall and Chadderton 1999; Waters and Wallis 2000, 2001a, b; Waters et al. 1999, 2001; Esa et al. 2001; Wallis et al. 2001; Wallis and Waters 2003; Burridge et al. 2006). However, extensive attempts to link the observed genetic diversity with the morphologies and distributions of these lineages have proved difficult, or a failure (McDowall and Hewitt 2004; McDowall 2006a; Crow et al. 2009a) and it sometimes seems as though there is more morphological diversity *within* individual lineages than there is *among* closely-related lineages, i.e., there are sometimes more morphological differences between populations from within lineages but living in distinctly different habitats, than there are morphological differences between the various lineages living in similar habitats, despite their different ancestries. Morphological evidence indicates an original derivation of all these lineages from the diadromous koaro. Waters and Wallis (2001a, b), based on evidence from mtDNA, have suggested that there may have been dual derivations from koaro, i.e., what have become known as ‘flathead’ and ‘roundhead’ morphs within the complex may have separate derivations. However, later studies of nuclear DNA are providing somewhat different results, including the likelihood that all lineages in this group form a monophyletic clade, with only a single derivation from the diadromous koaro (*Gl. brevipinnis*) (Waters et al. submitted). This question needs further clarification. Townsend and Crowl’s (1991) demonstration of likely major range retreat of the various Taieri River galaxiid lineages in this species complex, in the face of invasion by introduced brown trout (*Salmo trutta*), indicates that it is almost certain that various of these lineages were once present much more widely than they are today (see also McDowall 2006b).

These c. 10 ‘roundhead’ and ‘flathead’ lineages form what seem to be two distinct lineages that some DNA sequence studies suggest form separate groups that have become generally known as ‘roundheads’ and ‘flatheads,’ though their precise relationships still remain uncertain and in a state of flux. These lineages together, provide the richest local/regional diversity of non-diadromous species seen anywhere amongst New Zealand’s rather sparse freshwater fish fauna. It seems doubtless no coincidence that this diversity is substantially centred on the submontane countryside of central Otago, as this is an area that represents one of the more substantial geographical areas that may have remained above the sea during the major marine transgression of the New Zealand area in the Oligocene (see Fig. 3.2) (Fleming 1979; Cooper and Millener 1993; Gibbs 2006 – but see Campbell and Hutchings 2007; Landis et al. 2008, for discussion of the prospect that there was complete Oligocene inundation of the New Zealand landscape). Even if New Zealand did become completely submerged in the early Cenozoic, this area of Central Otago is still an ancient land area compared with the rest of contemporary New Zealand. And although both morphological and molecular studies all link these lineages to the diadromous koaro (see Fig. 7.7; McDowall 1970; Waters and Wallis 2001a, b), neither the phylogenetic nor

the biogeographic evidence yet allows a confident reconstruction of the events relating to generation of this diversity.

Molecular studies, which were primarily responsible for establishing our understanding of the lineage diversity of this species group in a new light (King and Wallis 1998; Wallis et al. 2001; Esa et al. 2001; Wallis and Waters 2003; Waters and Wallis 2000, 2001a, b; Waters et al. 1999, 2001; Burridge et al. 2006), suggest the following distribution patterns.

11.2.1 Northern Flathead Galaxias: Widespread in the Northern South Island

Northern flathead galaxias (Fig. 11.2 – red symbols) is found in the northern South Island; this lineage has not yet been formally recognised taxonomically. It is found to the west of the Southern Alps, only in the headwaters of the Buller River system – in the Maruia and Rappahannock Rivers (Fig. 11.2, arrow 2). It is also in the Motueka River further north (arrow 2), and is then found in the Wairau, Awatere and Clarence Rivers that lie amongst, or to the north-west of, the Kaikoura Ranges. It seems curious that northern flathead galaxias has failed to disperse downstream in both the Buller and Motueka Rivers (but this is comparable with the way Canterbury galaxias has largely failed to spread downstream in most of the rivers of the eastern South Island – see below). Presumably we are here looking at some issues of habitat suitability, perhaps water temperatures that are preventing spread of northern flathead down the Buller River.

This distribution pattern of northern flathead may be a result of, or at least was influenced by, events that took place during or after the uplift of mountains of the northern South Island. Waters and Wallis (2000) estimated separation of populations northern flathead in the upper Buller River system from ‘northern’ populations elsewhere in the northern South Island (in the headwaters of the north-eastern or eastern flowing Wairau, Awatere and Clarence Rivers), as c. 0.3–1.2 million years ago, when there was certainly substantial mountain building going on in the area. It also means that the Buller River populations split from other northern flathead populations probably before the repetitive series of glaciation events during the Pleistocene, or certainly before the last major glacial advance, this being only 100,000 years ago. This means that it is unlikely that the existing Buller River populations were in the area throughout the glaciations and that the distribution patterns that we now observe in the Buller River must have developed since the glaciation. This, in turn, suggests that contemporary distribution patterns in the upper Buller River (Maruia and Rappahannock Rivers) are a response to events that are much more recent than those related to the lineage-split, itself. And, if that is accepted, then we should then not expect to be able to explicitly link existing fish distribution patterns to geomorphological events that might have contributed to the lineage split. Rather, existing distributions should be viewed as a secondary, post-Pleistocene response to history of the river catchment connections, substantially including the effects of advance and retreat of the glaciations.

There has in the past been discussion of the likelihood that the Maruia River captured a headwater tributary of the east flowing Waiau River (Soons 1992), and it was long ago suggested that the presence of populations of the *Galaxias vulgaris* species complex in the upper Maruia River is a response to such a stream capture (McDowall 1970). However, given the likelihood of the long period of repetitive glaciations in the area, just discussed, it seems highly unlikely that this stream capture had anything to do with the *Galaxias vulgaris* species complex getting into the upper Buller. Moreover, molecular studies (Waters and Wallis 2000) show that the *Galaxias vulgaris* complex lineage in the upper Waiau is Canterbury galaxias, and so is not closely connected to the Buller River populations of northern flathead. Waters and Wallis (2000) showed that the Maruia population has only a single haplotype, which suggests that the population is based on a very small propagule, either resulting from very few fish getting into the Maruia River from where ever it originated or/and that the population went through a severe bottleneck at some time. This conclusion indicates the need for additional exploration of the area to search for possible additional populations and for clarification of the lineage status of any populations that are discovered, before it is possible to understand the history and geography of northern flathead in the area.

Northern flathead is also in the upper reaches of the north-flowing Motueka River, and this presumably reflects ancient fluvial connections between that river's headwaters and the Wairau River further to the east, quite probably the result of an upper tributary of the Motueka connecting at some time to the Wairau in the vicinity of Tophouse (where northern flathead is widespread). Craw et al. (2008) discuss complex changes in fluvial patterns and connections in this area, implicating parts of the Buller, Motueka, Wairau and other river systems, and the distribution of northern flathead; may relate to these. The details are presently unresolved.

The observation that these lineages within the *Gl. vulgaris* species complex are, with only minor exceptions, all found east and north of the main mountain ranges of the South Island, might suggest that the group's history of spread and diversification, at least to the north, post-dates the uplift of the Southern Alps that began only in the Pliocene, and which continues, today (Whitehouse and Pearce 1992). Wallis and Trewick (2009: 3,663) suggest that "west coast populations [of these lineages] were expunged by glaciation," though explicitly what they meant is unclear. There is no evidence that members of this species complex ever occupied west coast rivers beyond the upper Maruia River and the nearby Rappahannock. Additional DNA sequencing studies are needed before any additional clarity about the origins and distributions of these populations can be obtained.

11.2.2 Canterbury *Galaxias*, *Galaxias vulgaris*, a Canterbury Endemic

Canterbury galaxias (*Gl. vulgaris* sensu stricto – Fig. 11.2 – grey symbols) occurs in rivers of the eastern South Island to the south of those mentioned in Section 11.2.1) above – at its northern range limits it is found in the coastal catchments of the Seaward Kaikoura Ranges, in the Conway River, and southwards (Fig. 11.2, arrow

15). Further south, this lineage is found very widely, especially in hill country tributaries of the rivers that drain the eastern flanks of the Southern Alps and their foothills, and which flow across the Canterbury Plains, existing as far south as, and including, the Waitaki River (Fig. 11.2, arrow 13). There are quite numerous records from streams at, or even a little below, the upper fringes of the Canterbury Plains, though usually only occasional individuals have been found, and these populations may not be self-sustaining, but be derived by individuals, probably larvae and juveniles, that are carried downstream from the headwater populations, i.e., they may be reproductive sink populations (Pulliam 1988) that are expatriates from source populations in higher elevation streams in the intermontane valleys. Certainly, populations of these lineages do not seem to build up in the rivers out on the Canterbury Plains. Canterbury galaxias has by far the largest range of any of the lineages in this species complex, and exhibits molecular diversity and genetic structuring across the Canterbury Plains that seem to relate to geography (Wallis et al. 2001; Waters and Wallis 2000; Wallis and Waters 2003). Thus, its pattern of genetic diversity across this broad geographic range may imply northerly spread of the lineage across the Canterbury Plains during late Pliocene and Pleistocene, as the plains themselves were formed by erosion from the uplifting Southern Alps, and as gravels were carried from the terminal glacial moraines. Spread of this galaxiid was probably facilitated by the rivers wandering back and forth across the plains, as they formed, making varied, lateral connections between the major river systems (Waters et al. 2001). Changing connections between these river systems may also have taken place when lowered sea-levels resulted in the extension of the Canterbury coastline as much as 50 km further east than at present (Kirk 1994) (see Fig. 3.4). A yet further contribution to gene flow and lineage spread may have resulted from the populations of Canterbury galaxias being forced out on to the plains and/or held, downstream at lower elevations by Pleistocene glacial advances that filled the intermontane valleys with ice (Willett 1950; Gage 1958; Soons 1992). Canterbury galaxias appears likely to have moved upstream into these valleys following the most recent glacial retreat, perhaps only 10–15,000 years ago. Wallis et al. (2001) identified several distinct sub-lineages within a monophyletic assemblage of populations of Canterbury galaxias, that imply sequential northwards spread.

Canterbury galaxias is also present in a series of smaller coastal drainages south of the Waitaki River valley, in the Kakanui and Waianakarua Rivers (Fig. 11.2, arrow 12). These rivers drain coastal hills, including the Kakanui Mountains, south of the Waitaki River valley, and they lie east of the Maniototo Plains and the upper reaches of the Taieri River (where there are other members of this species complex – see Figs. 11.2 and 11.3, discussed below).

Further detailed studies of these river systems and their fish lineages is needed. Possibly, comparisons of patterns of relationship among other freshwater fish lineages, such as the pencil-galaxias species or the non-diadromous upland bully, may be informative (in particular, see later discussion of the distributions of the ‘pencil-galaxias’ complex in the upper Buller River, see Chapter 12).

How northern flathead and Canterbury galaxias (both ‘flathead’ lineages) relate to the two Otago-Southland roundhead/flathead galaxias species sub-complexes is not explicitly clear, though molecular evidence suggests that both are northern

representatives of the flathead morphotype (Waters and Wallis 2001b). Some aspects of these relationships are still unclear.

If Canterbury galaxias and northern flathead share a common ancestry, they are probably derived from an ancestral flathead stock that escaped from the Otago Peneplain, and spread north into the Waitaki River system. This might have been Taieri flathead penetrating north via the Kye Burn in the headwaters of the Taieri River (Fig. 11.3, arrow 17), or possibly Clutha flathead galaxias from the Lindis River (Fig. 11.3, arrow 1), an inland tributary of the Clutha River, further upstream, into the Ahuriri or Omarama Rivers, the latter being part of the upper Waitaki. Major uplift of the Southern Alps accelerated from about 5 million years ago (Whitehouse and Pearce 1992; McGlone et al. 2001), the erosion of these mountains leading to the formation of the Canterbury Plains, and this might provide some perspective on the earliest timing of the dispersal of these galaxiids.

11.2.3 Southern Flathead and Roundhead Lineages in the Southern South Island

Shifting attention south of the Waitaki River, into Otago and Southland, we encounter the much greater morphological and molecular diversity, and evolutionary/biogeographical complexity, of the Otago and Southland lineages of this species complex that fall into the two distinct 'roundhead' and 'flathead' morphs. Just how discrete these groups of lineages are remains somewhat unresolved, as noted above. Mitochondrial DNA studies have suggested that the two morphs may have separate derivations from a diadromous *Gl. brevipinnis* ancestry (Waters et al. 1999, 2001; Wallis et al. 2001; Waters and Wallis 2001a, b; Esa et al. 2001), but studies of nuclear DNA are suggesting somewhat different relationships possibly involving a single derivation from *Gl. brevipinnis* (Waters et al. submitted). Clarifying this question does not impact seriously on exploring the distributions of the various lineages, discussed below, and possibly there were alternative patterns of relationships among the lineages that are yet to be clarified.

The lineages from within each of the roundhead and flathead lineage groups are generally allopatric, as would be consistent with various of the members evolving in different areas/catchments that attach, in some measure, to the major river systems of the area. Lineages in the east- to south-east-flowing Clutha and Taieri Rivers seem, in general, well separated geographically from those in the south-flowing rivers of the Southland Plains, the latter connecting also further south to Stewart Island (which had land connections to Southland during the lowered sea levels of the Pleistocene: Fleming 1979) (see Fig. 3.4, arrow 7, p. 62) and possibly there were confluent river systems between Southland and Stewart Island at that time.

There is what might be a small area of overlap between Canterbury galaxias and the more southern lineages in the Shag River, another small coastal drainage south of the Kakanui River, where the identity of lineages remains somewhat unresolved (Fig. 11.2, arrow 12). There seems to be what is known as Taieri flathead galaxias (found primarily to the east in the upper Taieri) in the upper reaches of the Shag,

and these could result from inadvertent anthropogenic transfers related to water races constructed in the area by nineteenth century goldminers that could have brought fish from the upper Taieri eastwards into the upper Shag River catchment. Other populations in the lower tributaries of the Shag (Hellene Creek, Tipperary Creek, McCormick's Creek); also in Trotters Creek (a small independent coastal catchment a little north of the Shag: Fig. 11.2, arrow 12), are of even more uncertain ancestry, and could be Taieri flatheads, though they could be hybrids of presently undetermined provenance. Further work is needed on these fish populations. Taieri flathead galaxias + *Galaxias* 'Teviot' form a sister clade of all other flathead lineages (northern, Canterbury, Clutha, and Southland flatheads – see Fig. 7.7).

I now look first at the distributions of these various lineages in detail, and then explore some anomalies or zones of overlap.

11.2.4 Taieri Flathead Galaxias, *Galaxias depressiceps*, a Largely Taieri River Endemic

Taieri flathead galaxias (*Gl. depressiceps* – Fig. 11.3 – red symbols) is found primarily in the upper Taieri River, where it is restricted largely to the upper, higher-elevation tributaries, and spread downstream in the Taieri only as far as the Nenthorn Stream and Three O'Clock Stream, near Middelmarsh (Fig. 11.3, arrow 15). Taieri flathead has also spread eastwards, however, into the headwaters of some small coastal catchments, the Shag (Jimmys and Deepdell Creeks, as discussed on p. 267) and into the Waikouaiti River (Back Creek). In addition, there are highly disjunct populations of Taieri flatheads a little further south in the Narrowdale, a lower Tokomairiro River tributary (Fig. 11.3, arrow 11; Fig. 11.4, arrow 9), and in Akatore Creek, a small, independent coastal stream just south of the mouth of the Taieri River (Fig. 11.3, arrow 12; Fig. 11.4, arrow 10). The biogeographical significance of the Narrowdale and Akatore populations is at present uncertain, but they are clearly oddities. Taieri flathead is thus primarily a Taieri River endemic, and appears to share a common ancestry with further flathead lineages.

Formerly, further flathead galaxias populations there across the Clutha River system, and in the rivers of the Southland Plains, were regarded as belonging with Taieri flatheads (McDowall and Wallis 1996), but this is now rejected by molecular data (Waters and Wallis 2001b; and see McDowall 2006a), and they are now regarded as distinct lineages, discussed below.

11.2.5 Clutha Flathead Galaxias, *Galaxias* 'Species D', in Central Otago

Clutha flathead galaxias (at present not formally named or described) (Fig. 11.3 – blue symbols) is one of these flathead lineages, many of its populations having formerly been referred to as *Gl. depressiceps* (McDowall and Wallis 1996).

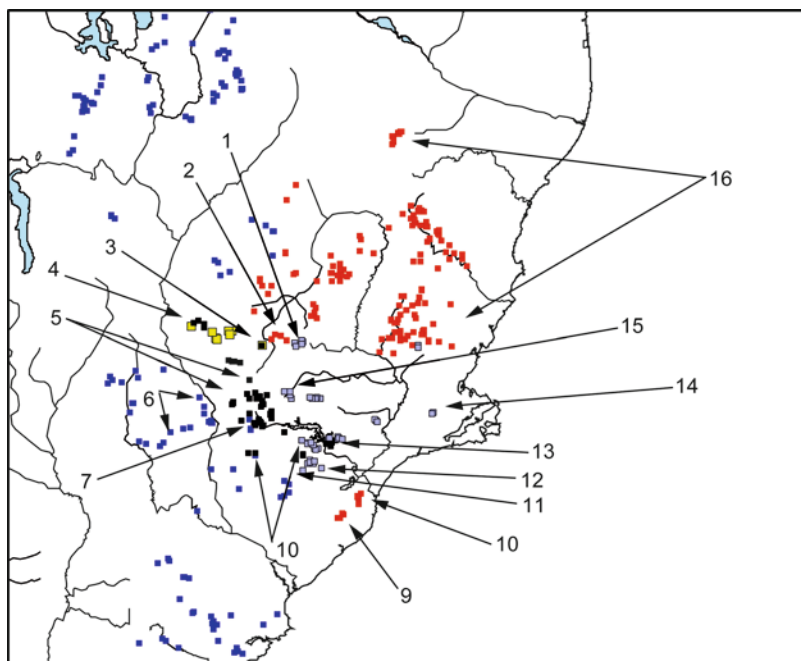


Fig. 11.4 Detail in the distributions of the several lineages in the *Galaxias vulgaris* species complex in the Waipori River and nearby sub-catchments of the Taieri, Clutha and Tokomairiro Rivers: Eldon's galaxias, *Gl. eldoni* (■); dusky galaxias, *Gl. pullus* (■); Taieri flathead galaxias, *Gl. depressiceps* (■); Teviot galaxias, *Galaxias* 'teviot' (■), Clutha flathead, *Galaxias* 'species D' (■). Arrows – ↑1: Suttons/Stony Streams; ↑2: upper Taieri; ↑3: Red Swamp Creek, upper Taieri; ↑4: Teviot River; ↑5: Beaumont River tributaries; ↑6: mid-Clutha tributaries; ↑7: Tuapeka River; ↑8: Waitahuna River tributaries; ↑9: Narrowdale Stream, Tokomairiro River; ↑10: Akatore Stream; ↑11: Tokomairiro River; ↑12: Meggat Burn, tributary of Lake Waipori, lower Taieri River; ↑13: Waipori River tributaries and Lake Mahinerangi; ↑14: Whare Creek, a lower Taieri tributary; ↑15: Canton Creek, lower Taieri River; ↑16: mid-lower Taieri tributaries

It has a complementary distribution with Taieri flatheads (*Gl. depressiceps*) in Central Otago – being found widely across the Clutha River system, from head-water streams like the Lindis River (Fig. 11.3, arrow 1) and Cardrona (Fig. 11.3, arrow 2), downstream, towards the Clutha mouth, and including tributaries of the Pomahaka (Fig. 11.3, arrow 10), and elsewhere, where there are suitable streams; it is also found in the Manuherikia River, a northern tributary of the middle reaches of the Clutha River (Fig. 11.3, arrow 16). Thus, it is substantially a 'Clutha endemic', though it extends a little south beyond the Clutha River to be quite widespread in streams draining the southeastern (coastal) flanks of the hills of the Catlins area (Beresford and McLennan Range: Fig. 11.3, arrow 9).

11.2.6 *Teviot Flathead Galaxias, Galaxias ‘Teviot’, a Localised Lineage*

Teviot galaxias is another unnamed and undescribed flathead lineage that is, as its common name indicates, found primarily in the Teviot River, a tributary of the middle Clutha a little downstream from Roxburgh (Fig. 11.3 – yellow symbols), where its distribution overlaps with that of dusky galaxias, though no site sympatry is known. There is also a population of Teviot galaxias in Red Swamp Creek, an upper Taieri River tributary across a low divide with the upper Teviot River (Fig. 11.3, arrow 14; Fig. 11.4, arrow 3), where some stream capture event seems likely; there it is sympatric with a population of dusky galaxias. Teviot galaxias is a lineage related to Clutha flathead galaxias (Fig. 11.3 – blue symbols), and these two forms are together a sister lineage to Taieri flathead galaxias from the upper Taieri (Fig. 11.3 – red symbols).

11.2.7 *Southern Flathead Galaxias, Galaxias ‘Southern’, in Southland and Stewart Island*

Southern flathead galaxias is yet another flathead-related (unnamed, undescribed) lineage (Fig. 11.3 – green symbols) that was also formerly included in *Gl. depressiceps* (McDowall and Wallis 1996), and which is present widely in south-flowing rivers of the Southland Plains – primarily from the Oreti in the east (Fig. 11.3 arrow 6) west as far as the Waiau River (Fig. 11.3, arrows 5). It is, however, widely lacking from the Mataura River, being present mainly in its uppermost headwater streams, prompting the prospect that these Mataura tributary streams were formerly connected to the upper Oreti River, perhaps in much the same way as the Oreti and Waiau were once connected according to BurrIDGE et al. (2008).

This lineage is also present on Stewart Island (Fig. 11.3, arrow 7).

There are what seem to be anomalous, rather disjunct Mataura populations of this lineage in the Garvie Burn, a tributary of the Waikaia River and in the headwaters of the Mokoreta River, a southeastern tributary of the lower Mataura River that drains from the western flanks of the McLennan Range in the Catlins district (Anderson 2007). There are no other populations of this lineage anywhere in the mid and lower Mataura, the nearest populations being those in the upper reaches of the Mataura, discussed above. So, these populations are somewhat enigmatic and presently elude convincing explanations, though in a way it is the absence of this lineage across most of the lower and middle Mataura that is most surprising.

Southern flathead galaxias is not present anywhere in the Clutha River system, apart from a population in a tributary of the Von River that now flows into the southern shores of Lake Wakatipu (Fig. 11.3 – green symbols, arrow 4), and so is essentially a part of the Kawarau River catchment. However, the Von formerly drained south to join the upper Oreti River (Craw and Norris 2003; BurrIDGE et al. 2006). Interestingly, Gollum galaxias (see below) is present in different Von tributaries (Fig. 11.2 – black symbols, arrow 6) and the presence of the two lineages in

the Von could reflect separate headwater capture events. The observed southern affinity of the roundhead lineage in the Von River is consistent with such an Oreti connection (Burridge et al. 2006). There appears now to be one very low divide between the upper Von (that flows northeast) and the Oreti's Hidden Burn (which flows southwest), and another between the Path Burn, another Von tributary and higher reaches of the Hidden Burn (Burridge et al. 2006). Thus this rather disjunct, isolated, presence of both southern and roundhead galaxias in the Von have the 'ring' of novel biogeographical events – again, evidence of an ancient river capture there.

11.2.8 Central Otago Roundhead Galaxias, *Galaxias anomalus*, Widespread in Both the Clutha and Taieri River Systems

There is a series of additional lineages, generally referred to as 'roundheads' that are found widely across Otago and Southland. There is a widespread view that roundheads tend to live upstream of flatheads, but I think that this is, rather, a question of different habitat preferences and habitat availability – the roundhead morph is found in small, shingly streams, rather than in streams with rather coarser cobble/boulder substrates, and may be present well downstream where there are shingly substrates, e.g., there is a population of southern roundheads in a stream draining into the tidal estuary of the Waiau River in western Southland.

Central Otago roundhead galaxias (*Gl. anomalus* – Fig. 11.2 – light green symbols) is found primarily in the upper reaches of the Taieri River (just to the south of the Waitaki River and west of the Kakanui, Shag, and Waianakarua Rivers); the Central Otago roundhead extends downstream in the Taieri only as far as about Middlemarch in the mid Taieri (Fig. 11.2, arrow 11), and is also quite widely present, to the west of the Taieri River catchment, in the Manuherikia River, a south-flowing northern tributary of the middle Clutha River catchment (from where this species was originally described – Stokell 1959) (Fig. 11.2, arrow 3).

In addition to the effects of introduced trouts on these galaxiid lineages generally, abstraction of water for irrigating pastoral lands in the Manuherikia River valley, may have dewatered streams and have greatly reduced this lineage's geographical spread. Roundhead populations from streams of the Southland Plains, which were formerly included in this species (McDowall and Wallis 1996), are now regarded as Gollum galaxias (see next section) (Fig. 11.2 – black symbols: Waters and Wallis 2001b).

11.2.9 Gollum Galaxias, *Galaxias gollumoides*, a Southern Roundhead, Widespread Across Southland and Stewart Island

Very similar, and closely related, to Central Otago roundhead galaxias, is Gollum galaxias (*Gl. gollumoides* – Fig. 11.2 – black symbols), which molecular studies are showing to be present widely in almost all of the rivers across the Southland Plains,

i.e., from the southeastern rivers that drain the McLennan Range of the Catlins district (Fig. 11.2, arrow 10), westwards across the Southland Plains as far as the Waiau (Fig. 11.2, arrow 8); this species is present also on Stewart Island (Fig. 11.2, arrow 9), from where it was first described (McDowall and Chadderton 1999).

With two distinctive exceptions this roundhead morphotype is absent from the entire upper-mid Clutha River. One of these exceptions is a population in the Nevis River, which flows north in a valley between the Remarkables and Garvie Mountains to join the Kawarau River, a major inland Clutha River tributary (Fig. 11.2, arrow 5) (Waters et al. 2001; Wallis and Waters 2003). Waters et al. (2001) have described how the Nevis River, which now flows north down the Nevis valley and cuts through a steep gorge to join the Kawarau, formerly flowed south to join the headwaters of the Nokomai River of the Mataura River catchment (Craw and Norris 2003). A river capture event is believed to have taken place as a result of differential uplift, following which the Nevis cut its gorge to the Kawarau.

In addition, there is a population of Gollum galaxias (discussed in Section 11.2.7) in a tributary of the Von, a different tributary from that where southern flathead is known, and this Gollum population seems likely to have entered the Von via a river capture event, possibly a different capture event from the one discussed above for Gollum galaxias that allowed southern flathead entry to the Von. Or, if it results from the same capture event, it seems likely that there has been competitive displacement resulting in Gollum galaxias and southern flatheads now occupying different upper Von tributaries.

The ‘roundhead’ morph, whether *Gl. anomalus* or *Gl. gollumoides*, other than in the Nevis and Von Rivers, and those in the Manuherikia River, is generally absent from the Clutha River system. Genetic evidence shows that two populations in tributaries of the Pomahaka River, that were once regarded as Central Otago roundhead galaxias (McDowall and Wallis 1996), are Clutha flatheads (Jon Waters, pers. comm.), an example of the extent to which morphological characters seem plastic, making separation and identification of individual populations difficult.

11.2.10 Dusky Galaxias, *Galaxias pullus*, a Roundhead Lineage in the Lower Taieri River

Dusky galaxias (*Gl. pullus* – Fig. 11.3 – black symbols, arrow 13 and Fig. 11.4 – black symbols) is probably a roundhead morph, and is present primarily in tributaries of the Waipori River, itself a major southwestern (inland) tributary of the lower Taieri River. However, this species has also been found in several contiguous surrounding catchments:

1. In the uppermost, headwaters of the Taieri (Red Swamp Creek: Fig. 11.3 – yellow symbols, arrow 14; Fig. 11.4, arrow 3) to the east.
2. In tributaries of the Clutha River to the northwest of the upper Waipori (the Teviot River: Fig. 11.4, arrow 4).

3. In the Beaumont River (Fig. 11.4, arrow 5) and Tuapeka River (Fig. 11.4, arrow 7) to the south-west.
4. In the Waitahuna River to the south (Fig. 11.4, arrow 10).
5. Also in the Tokomairiro River, a small, independent catchment that drains landscape to the south of the lower Taieri/Waipori and north of the Clutha (Fig. 11.4, arrow 13).
6. There is a population of the lineage in Red Swamp Creek, a tributary of the uppermost Taieri River (where there is also a population of *Galaxias* ‘Teviot’ – Fig. 11.4, arrow 3, but how this distribution developed is undetermined, as yet.

This species, as well as Eldon’s galaxias (see next paragraph), were hitherto both regarded as having affinities with Central Otago roundhead and Gollum galaxias (Waters and Wallis 2001b). Again, however, nuclear DNA is indicating alternative patterns of relationship, suggesting that these populations are rather more distant (Waters et al. submitted) – possibly, with Eldon’s galaxias, a sister-group to all other non-diadromous members of the group.

11.2.11 *Eldon’s Galaxias, Galaxias eldoni, a Second Roundhead Lineage in the Lower Taieri*

Eldon’s galaxias (*Gl. eldoni* – Fig. 11.2 – light blue symbols and Fig. 11.4 – light blue symbols) has a quite broad and fragmented distribution in the lower Taieri, being found in:

1. Western tributaries of the mid/lower Taieri downstream of Middlemarch, in Lee Stream and Sutton Stream (Fig. 11.4, arrow 15)
2. In one eastern tributary, Whare Creek that connects to the Silver Stream (Fig. 11.4, arrow 14)
3. In tributaries of the Waipori, where it and dusky galaxias tend to have complementary distributions (Allibone 1999: Fig. 11.4, arrow 13)
4. In the Meggat Burn, a western (inland) tributary of Lake Waipori (Fig. 11.4, arrow 12)
5. In headwaters of the east and west branches of the Tokomairiro River a little south of the lower Taieri (Fig. 11.4, arrow 11)

Dusky and Eldon’s galaxias thus comprise two largely lower, but inland, Taieri endemics (found widely across the Waipori sub-catchment of the southern limb of the Taieri River), and they both give the impression of having ‘spilled over’ into various surrounding catchments to the north, west and south – though molecular studies are needed to explicitly determine the sources and directions of movement of the various populations. It is interesting that, in general, there is no geographic overlap (nor are there geographical/dispersal barriers) between:

1. Populations of Eldon’s galaxias and dusky galaxias in the lower Taieri and its tributaries.

2. Central Otago roundheads and Taieri flatheads in the upper Taieri. These two groups are entirely allopatric, though there is an instance of near sympatry of *Gl. pullus* and Teviot galaxias in the very headwaters of the Taieri (Red Swamp Creek – Fig. 11.4, arrow 3), into which both lineages seem to have spread from catchments to the south.

11.3 Process and Pattern in the *Galaxias vulgaris* Species Complex

These various *Gl. vulgaris* complex lineages exhibit patterns of distribution having a series of fascinating explanations that seem to relate to the earth history of the eastern and southern South Island, some of the more simple and explicit scenarios being discussed above. However, some of the distribution patterns defy simple explanation.

There is interesting, broad and distinctive overlap of these Otago/Southland flathead/roundhead lineages in the eastern Catlins area, in rivers draining to the southeastern coast of the South Island of New Zealand from the McLennan Range. Roundhead Gollum galaxias populations in the Catlins area (Fig. 11.2, arrow 10) are related to others in Southland, to the south and west (Fig. 11.2, arrows 7, 8), whereas flathead populations in the Catlins area (Fig. 11.3, arrow 9 – blue symbols) belong to Clutha flatheads and connect to the Clutha catchment to the north-west; Fig. 11.3, arrow 10), indicating some individualistic dispersal processes, that have converged in the Catlins district from dual directions.

Extension of the geographical range of Central Otago roundhead galaxias from the upper Taieri, westward into tributaries of the Manuherikia (Clutha River), to the west (Fig. 11.2, arrow 3 – light green symbols), raises the prospect that at some past time the upper Taieri River may have flowed west into the Manuherikia catchment rather than connecting, as it does now, with the southern parts of the Taieri. There is, however, somewhat of a paradox in there being a single, widespread roundhead lineage in the upper Taieri that extends westwards across the Rough Ridge Mountain Range into the Manuherikia (Fig. 11.2, arrow 3; Fig. 11.4 – red symbols), whereas there are separate, distinct, flathead lineages in the two catchments on each side of the Rough Ridge (Taieri flathead in the Taieri and Clutha flathead in the upper Manuherikia). Has, then, a single vicariance event (uplift of the Rough Ridge), had two different outcomes for flathead and roundhead lineages; or are we looking at an initial vicariance event (the two flathead lineages), and a later dispersal across the Rough Ridge (either east-west or west-east) by Central Otago roundhead galaxias? Other more complex, less parsimonious, hypotheses could be imagined, such as later invasion by Clutha flatheads up the Manuherikia River, to establish sympatry with Central Otago roundheads. Genetic studies might be informative.

The presence of two, distinct, lower-Taieri/Waipori endemics (dusky and Eldon's galaxias – both possibly roundhead lineages), largely separate from stocks of the *Gl. vulgaris* species complex in the upper Taieri River, might also suggest that the

upper and lower Taieri Rivers were once parts of separate catchments. The lack of suitable habitats for these fish more widely in the Taieri seems an unlikely explanation for the restricted ranges of the two groups of lineages (there are no marked differences between the streams across this area – and especially given the disjunct population of Taieri flatheads in Akatore Creek (an independent coastal catchment) and the Narrowdale Stream (tributary of the Tokomairiro River) near sea level, a little south of the Taieri River mouth (Fig. 11.3, arrows 12 and 11; Fig. 11.4, arrows 10 and 9). So, there are some enigmatic patterns, in addition to others that seem to be ‘common sense’. There is dual evidence for fluvial connections between the upper Taieri and rivers to the south, especially the Clutha River. Also, there are populations of ‘Teviot’ galaxias perhaps from the Teviot River, and dusky galaxias probably from the upper Waipori River, both being recorded in Red Swamp Creek in the uppermost Taieri.

The fact that both Central Otago roundhead and Taieri flathead galaxias extend down the Taieri River system only to about Middlemarch (Fig. 11.2, arrow 11; Fig. 11.3, arrow 15) may also raise the prospect that the mid-Taieri River may once have flowed north rather than south (and could then have connected west to the Manuherikia, part of the Clutha catchment). This would be consistent with the suggestion, made above, that the upper Taieri may once have flowed west to the Manuherikia, and have been quite separate from the lower Taieri River catchment below about Outram or Middlemarch.

There are other apparent pattern conflicts. Teviot galaxias is possibly a sister lineage of [Southland flathead galaxias and Clutha flathead], and is clearly a divergent, locally-distributed, flathead lineage found primarily in the Teviot River (mid-Clutha catchment). ‘Flatheads’ are otherwise represented by two further distinct lineages across the Clutha and Taieri catchments – one in the Taieri catchment (Taieri flathead galaxias), which is genetically distinct from Clutha flathead (that is widespread through the upper and mid- Clutha – Lindis and Cardrona Rivers: Fig. 11.3, arrows 1 and 2, and in the lower Clutha: arrow 10).

Thus, the taxonomic diversity and distributions of the various lineages involved in the *Gl. vulgaris* species complex south of the Waitaki River (the southern limits of Canterbury galaxias) are themselves complex. What is of most interest, for the present, is that in several instances the various local scenarios reflect existing or historic geological and geomorphological events that make some sense of the diversity, whether this is recognised in formally described species, or just as distinct lineages indicated by molecular data.

Craw et al. (1999) show a “Fiordland boundary fault” in the southwestern South Island, and this coincides with the western margin of the distribution of both Gollum galaxias (Fig. 11.2, arrows 6 and 7) and southern flathead lineages in the Waiau River in western Southland; Fig. 11.3 – green symbols, arrow 5). However, it is probably far-fetched to causally link the presence of the fault with galaxiid distributions. It seems far more likely that this is as far west as the members of this species group have been able to spread since the last retreat of glacial ice in the Pleistocene. Burridge et al. (2006) reported Waiau populations of southern flathead galaxias in the Waiau River to be somewhat genetically distinct from others in the

Oreti, Aparima, and Mataura Rivers across the central and eastern Southland Plains, and Stewart Island, as well as that in the Von, with populations from these various rivers not forming monophyletic clades. These points imply complex patterns of between-drainage dispersal that are not at present understood.

One curious anomaly is that, apart from:

1. The population of Southland Gollum roundheads in the Nevis River (Waters and Wallis 2000) (Fig. 11.2, arrow 5)
2. Both Gollum galaxias (Fig. 11.2, arrow 6) and southern flatheads in the Von (and in different Von tributaries (Fig. 11.3, arrow 4), Burridge et al. 2006)
3. A population of Clutha flathead in the Bannock Burn just upstream of the confluence of the Kawarau and Clutha Rivers (Fig. 11.3, arrow 3, and see Fig. 11.5)

there are no populations of any of the *Gl. vulgaris* species complex anywhere in the Kawarau branch of the Clutha River – even though other inland tributaries of the mainstem Clutha have prolific populations of this complex. This also may well be a heritage of Pleistocene glaciation, and the associated changes in flow directions from Lake Wakatipu. The lake once drained via its southern arm into the upper reaches of the upper Oreti River, but with the deposition of large amounts of gravel carried south during the last glacial advance, the southern discharge of Lake Wakatipu was occluded at glacial retreat, and the lake now drains east from its middle arm via the Kawarau River into the Clutha catchment. The presence of Central Otago flatheads in the Bannock Burn, now a tributary of the Kawarau River, near Cromwell (Fig. 11.5), is distinctive in being the only population in the Kawarau of a galaxiid with Clutha River provenance. This may well be due to the Bannock Burn having been connected to the mainstem Clutha River, prior to the formation of the Kawarau and its role in draining Lake Wakatipu to the east. The Kawarau River would have ‘picked up’ the lower Bannock Burn as it penetrated east to join the Clutha mainstem. Note that there is a very abrupt change in the direction of the flows of the Kawarau at the point where it is joined by the Bannock Burn (Fig. 11.5) which I consider highly indicative of the pre-existing channel of the Bannock Burn itself.

Various of these *Gl. vulgaris* lineages are found together or in close proximity in a number of localities, but sympatry usually involves the co-occurrence of a flathead lineage with a roundhead. If Townsend and Crowl’s (1991) allegations of extensive range reduction as a result of invasion by trout are correct, there is a prospect that, prior to trout introductions (McDowall 2006b), there were formerly many more instances of two lineages either occurring in sympatry or in close proximity to each other; i.e., to some extent we may now be looking at headwater, refugial, isolates of species that were probably once much more widespread. When these lineages are naturally sympatric, hybridisation is either absent (Waters et al. 2001; Crow et al. 2008; Crow et al. 2009b) or very rare indeed (Allibone et al. 1996).

At the broadest scale, there is general range overlap between various of the roundhead and flathead lineages across most of Otago, Southland and Stewart Island (Figs. 11.2–11.4) and, as well, there are instances where the two lineages are either sympatric, or they share stream habitats in close proximity:

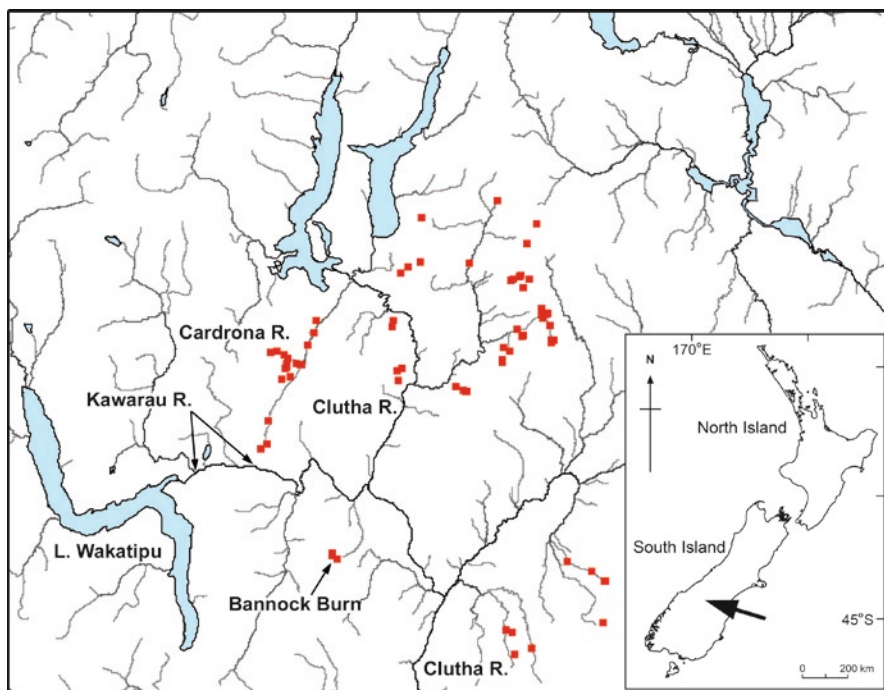


Fig. 11.5 Distribution of *Galaxias* 'species D' in upper Clutha River, inland South Island: note populations in Cardrona River and Bannock Burn

1. Central Otago roundhead and Taieri flathead galaxias have broadly complementary ranges in the upper Taieri; they are found together in upper headwaters of the Kyeburn River (Fig. 11.2 – blue symbols, arrow 14 and Fig. 11.3 – red symbols, arrow 17), where there are sites for Taieri flatheads within the broader range of Central Otago roundheads), and where molecular studies have revealed a very low level of hybridisation (Allibone et al. 1996; McDowall and Wallis 1996).
2. Central Otago roundhead and Clutha flathead are both present in Maori Creek an eastern tributary of the Manuherikia River draining the western flanks of the Rough Ridge (Fig. 11.3, arrow 16 shows localities for Clutha flathead which, again, lie within the western extent of the broad range of *Gl. anomalus*, in this instance in the Manuherikia catchment.
3. Southland flathead galaxias and Gollum galaxias are found together in a number of streams draining the upper Southland Plains: in different reaches of Excelsior Creek, a tributary joining the Waiau in western Southland, a little downstream from the confluence of the Waiau and Mararoa Rivers; their ranges, Gollum galaxias (a roundhead lineage) in the upper reaches and southern flathead galaxias in the lower reaches there, have not been explored in detail and there could be site sympatry; in the Mararoa River upstream of the Mavora Lakes in the upper Waiau; also in Princhester Creek another upper Waiau tributary; Irthing Stream,

an upper Oreti River tributary; both are also in close proximity in tributaries of the Eyre River, a headwater tributary of the Mataura River near Athol in northern Southland; both are, again, found together in Bushy Creek, a headwater tributary of the Mataura River (Waters et al. 2001).

4. Both dusky galaxias and Teviot galaxias are present in the Teviot River (Fig. 11.4 – black and yellow symbols, arrow 4) as well as in Red Swamp Creek in the uppermost Taieri (Fig. 11.4, arrow 3) with Taieri flathead galaxias also present a little further down the Taieri (Fig. 11.4, arrow 2); dusky galaxias and Teviot flathead are likely to have reached Swamp Creek from catchments to the south, whether together or separately is unknown; also these populations are in close proximity to populations of Taieri flatheads in the upper Taieri, though there is not site sympatry.
5. There are several known instances of natural co-existence of two lineages of either flathead or roundhead morphs. Dusky and Eldon's galaxias (both 'round-heads') occur widely and in close proximity in the reaches of the Waipori River

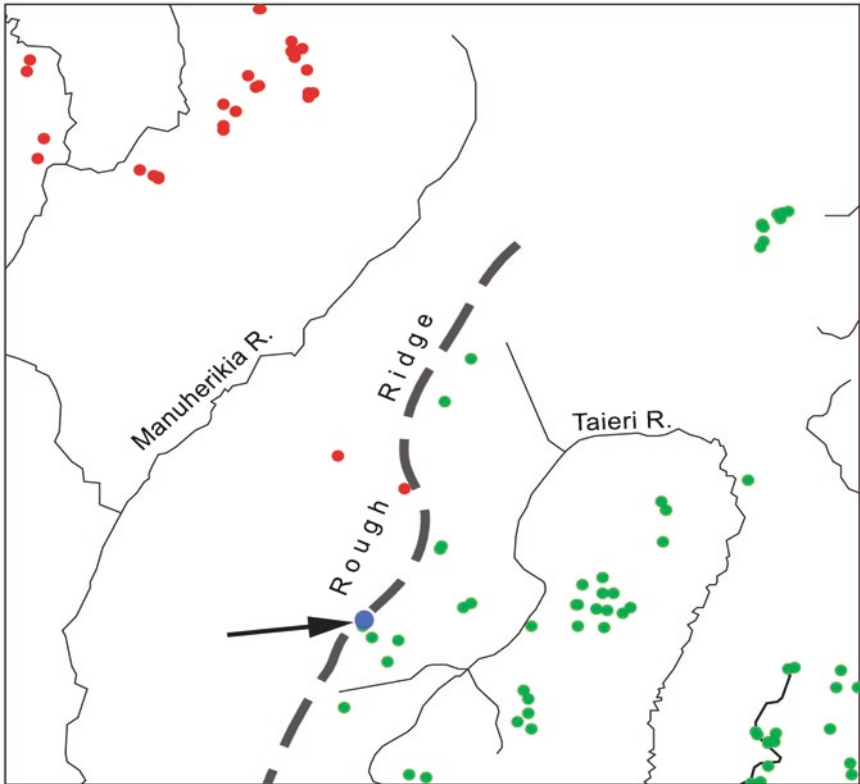


Fig. 11.6 Distributions of flathead galaxias lineages in relation to Rough Ridge Mountain Range (dashed line): Clutha flathead galaxias, *Galaxias* 'species D' (■); Totara Creek hybrid locality (■); Taieri flathead galaxias – arrowed; *Gl. depressiceps* (■)

close to the Lake Mahinerangi dam, and though their distributions there seem largely discrete and almost entirely complementary at the site scale they do exhibit some overlap (Allibone 1999) (Figs. 11.2–11.4).

6. Clutha flathead galaxias (Fig. 11.3 – blue symbols, arrow 9) and Gollum galaxias (Fig. 11.2 – black symbols, arrow 10), exhibit broadly overlapping distributions in streams draining to the southeast from the McLennan Range in the Catlins area and), and so here we see overlap between a flathead lineage, derived from the Clutha River system to the north and west, and a roundhead lineage of Southland, with provenance to the south and west.

In addition to the above there are instances where it seems either likely or possible that sympatry is anthropogenic:

7. Totara Creek is a stream in the upper Taieri River catchment where it is believed that artificial sympatry between Taieri flathead and Clutha flathead (hitherto called *Galaxias* ‘species D’) has been brought about by construction of water races by nineteenth century gold miners; the two lineages hybridise there (Esa et al. 2001; Allibone 2000) (Fig. 11.6 arrowed blue symbol).
8. There is also possible hybridisation between various lineages in the east-flowing upper Shag River (Fig. 11.2, arrow 12), though at present not enough is known to identify the parental lineages, or of the identity and relationships of populations in the lower Shag.

Thus, patterns of range-overlap point to distinct dispersal processes of these two lineages.

References

- Allibone RM (1999) Impoundment and introductions: their impacts on native fish of the upper Waipori River, New Zealand. *J R Soc N Z* 29:291–299
- Allibone RM (2000) Water abstraction impacts on the non-migratory galaxiids of Totara Creek. *Sci Conserv* 147:25–45
- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Allibone RM, Crowl TA, Holmes JM, King TM, McDowall RM, Townsend CR, Wallis GP (1996) Isozyme analysis of *Galaxias* species (Teleostei: Galaxiidae) from the Taieri River, South Island, New Zealand: a species complex revealed. *Biol J Linn Soc* 57:107–127
- Anderson L (2007) Geomorphology and freshwater fish biogeography of the Catlins Region, southern New Zealand. Unpublished MSc thesis, University of Otago, Dunedin, N Z, 103 pp
- Burridge CP, Craw D, Waters JM (2006) River capture, range expansion, and cladogenesis: the genetic signature of freshwater vicariance. *Evolution* 60:1038–1049
- Burridge CP, Craw D, Jack DP, King TM, Waters JM (2008) Does fish ecology predict dispersal across a river drainage divide? *Evolution* 62:1484–1499
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend CR (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 17–34

- Craw D, Youngson JH, Koons PA (1999) Gold dispersal and placer formation in an active, oblique collisional mountain belt, the Southern Alps, New Zealand. *Econ Geol* 94:605–614
- Craw D, Burrige CP, Upton P, Rowe DL, Waters JM (2008) Evolution of biological dispersal corridors through a tectonically active mountain range, New Zealand. *J Biogeogr* 35:1790–1802
- Crow SK, Closs GP, Waters JM, Wallis GP (2009a) Morphological and genetic analysis of *Galaxias* ‘southern’ and *G. gollumoides*: interspecific differentiation and intraspecific structuring. *J R Soc N Z* 29:43–62
- Crow SK, Closs GP, Waters JM, Booker DJ, Wallis GP (2009b) Niche partitioning and the effect of interspecific competition on microhabitat use by two sympatric galaxiid stream fishes. *Freshwat Biol*. doi:10.1111/j.1365-2427.2009.02330.x
- Douglas BJ (1986) Lignite resources of Central Otago: Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessments and exploration models. *N Z Energy Res Devel Comm Publ* 104:1–368
- Esa YB, Waters JM, Wallis GP (2001) Introgressive hybridization between *Galaxias depressiceps* and *Galaxias* sp. D (Teleostei: Galaxiidae) in Otago, New Zealand: secondary contact mediated by water races. *Conserv Gen* 1:329–339
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp
- Gage M (1958) Late Pleistocene glaciations of the Waimakariri valley, Canterbury, New Zealand. *N Z J Geol Geophys* 1:123–155
- Gibbs GW (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton, Nelson, N Z, 232 pp
- King TM, Wallis GP (1998) Fine-scale genetic structuring in endemic galaxiid fish populations of the Taieri River. *N Z J Zool* 25:17–22
- Kirk R (1994) The origin of Waihora/Lake Ellesmere. In: Davies J, Galloway L, Nutt AHC (eds) Waihora/Lake Ellesmere: past present future. Lincoln University/Daphne Brasell, Lincoln, N Z, pp 9–16
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Lee D, Forsyth J (2008) Central rocks: a guide to the geology and landscapes of Central Otago. *Geol Soc N Z Guidebook* 14:1–84
- Lee DE, McDowall RM, Lindqvist JK (2007) *Galaxias* fossils from Miocene lake deposits, Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *J R Soc N Z* 37:109–130
- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species; the ‘new’ biodiversity and evolutionary significant units among New Zealand’s galaxiid fishes. *J Fish Biol* 59(Suppl A):209–222
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1976) Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J R Soc N Z* 6:17–22
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1997a) Affinities, generic classification, and biogeography of the Australian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Rec Aust Mus* 49:121–137
- McDowall RM (1997b) Two further new species of *Galaxias* (Teleostei: Galaxiidae) from the Taieri River, southern New Zealand. *J R Soc N Z* 27:197–217
- McDowall RM (2000) The Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 224 pp
- McDowall RM (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Trans Amer Fish Soc* 132:229–238

- McDowall RM (2006a) The taxonomic status, distribution and identification of the *Galaxias vulgaris* species complex in the eastern/southern South Island and Stewart Island. NIWA Client Rep CHCDOC2006-081:1–40
- McDowall RM (2006b) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes. *Rev Fish Biol Fisher* 16:233–422
- McDowall RM, Chadderton WL (1999) *Galaxias gollumoides* (Teleostei: Galaxiidae), a new fish species from Stewart Island, with notes on other non-migratory freshwater fishes present on the island. *J R Soc N Z* 29:77–88
- McDowall RM, Hewitt J (2004) Attempts to distinguish morphotypes in the Canterbury-Otago non-migratory *Galaxias* species complex. *DOC Sci Int Ser* 165:1–18
- McDowall RM, Pole M (1997) A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J R Soc N Z* 27:193–198
- McDowall RM, Stevens MA (2007) Taxonomic status of the Tairāwhiti bully *Gobiomorphus alpinus* (Teleostei: Eleotridae), revisited – again. *J R Soc N Z* 37:15–29
- McDowall RM, Wallis GP (1996) Description and redescription of *Galaxias* species (Teleostei: Galaxiidae) from Otago and Southland. *J R Soc N Z* 26:401–427
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. *J R Soc N Z* 33:675–691
- McGlone MS, Duncan RP, Heenan PB (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J Biogeogr* 28:199–216
- Pulliam HR (1988) Sources, sinks and population regulation. *Am Nat* 43:187–193
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 439–455
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Stokell G (1959) Notes on galaxiids and eleotrids with descriptions of new species. *Trans R Soc N Z* 87:265–269
- Townsend CR, Crowl TA (1991) Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout. *Oikos* 61:347–354
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Wallis GP, Waters JM (2003) The phylogeography of southern galaxiid fishes. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend CR (eds) *The natural history of southern New Zealand*. Otago University Press, Dunedin, N Z, pp 101–106
- Wallis GP, Judge KF, Bland J, Waters JM, Berra TM (2001) Genetic diversity in New Zealand *Galaxias vulgaris* sensu lato (Teleostei: Osmeriformes: Galaxiidae): a test of a biogeographic hypothesis. *J Biogeogr* 28:59–67
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phylogen Evol* 37:417–425
- Waters JM, Wallis GP (2000) Across the Southern Alps by river capture? Freshwater fish phylogeography in South Island, New Zealand. *Mol Ecol* 9:1577–1582
- Waters JM, Wallis GP (2001a) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Wallis GP (2001b) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *J Fish Biol* 58:1166–1180
- Waters JM, Esa YB, Wallis GP (1999) Characterization of microsatellite loci from a New Zealand freshwater fish (*Galaxias vulgaris*) and their potential for analysis of hybridization in Galaxiidae. *Mol Ecol* 8:1080–1082
- Waters JM, Esa YB, Wallis GP (2001) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298

- Waters JM, Rowe DL, BurrIDGE CP, Wallis GP (in press) Gene trees versus species trees: reassessing life-history evolution in a freshwater fish radiation. *Syst Biol*
- Whitehouse IE, Pearce AJ (1992) Shaping the mountains of New Zealand. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 144–160
- Willett RW (1950) The New Zealand Pleistocene snow line, climatic conditions, and suggested biological effects. *N Z J Sci Tech* 32B:18–48

Chapter 12

Pattern and Process in the Distributions of Non-diadromous Species 2: The ‘Pencil-Galaxias’ Species Group

Abstract The ‘pencil galaxias’ species group includes five non-diadromous species that are widespread across central and southern New Zealand, with a centre of greatest diversity in the inland Mackenzie Basin of the eastern central South Island. They are small, very slender species of cold gravel rivers. Their geographical ranges relate closely to earth history, especially in the South Island, where some species’ ranges still reflect events during the Pleistocene glaciation, or reflect historical changes in river flow patterns. Absence of dwarf galaxias from South Westland reflects Pleistocene glaciation there, whereas absence in the northeastern North Island reflects Holocene to recent volcanism. Several pencil galaxias species are found widely in the inland, intermontane valleys of the eastern South Island, and probably penetrated them when Pleistocene glacial ice retreated. Dwarf galaxias is present on both sides of Cook Strait, probably a consequence of a land connection across the strait at lowered sea levels in the Pleistocene. Some species are present upstream of contemporary glacial lakes, and these distributions probably relate to riverine flow patterns during glacial retreat a few thousand years ago.

Keywords Alpine galaxias • Glaciation • Dwarf galaxias • Land connections • Longjaw galaxias • Pencil galaxias • Pleistocene

The group of very slender species (McDowall 1970), now referred to as the ‘pencil-galaxias’ species complex (McDowall and Waters 2003), comprises: alpine (Fig. 12.1), dwarf, bignose, upland longjaw, and lowland longjaw galaxias, of which bignose and lowland longjaw are only recently described (McDowall and Waters 2002, 2003). In addition to their general, distinctive, mutual similarity in general body form, these five species exhibit several fine details in osteology of both the cranium and pectoral girdle that imply a shared common ancestry, though not all of the molecular data are entirely consistent with that conclusion (McDowall 1969; McDowall and Waters 2002, 2003; author, unpublished), and further study of relationships is needed. This species group’s centre of diversity is the Mackenzie Basin of the upper Waitaki River system, where four of the

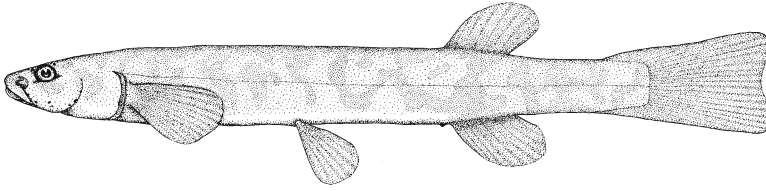


Fig. 12.1 Alpine galaxias, *Galaxias paucispondylus*, 70 mm LCF (family Galaxiidae), one of the 'pencil galaxias' species complex

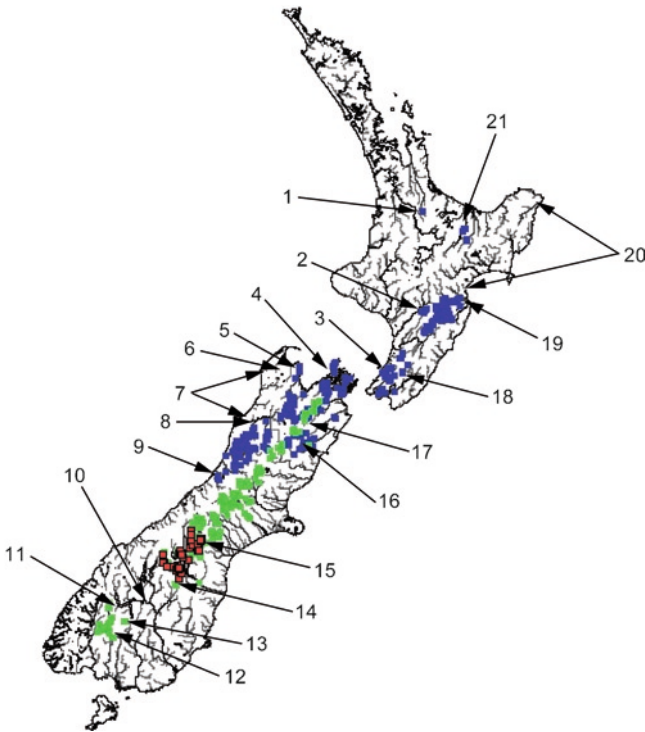


Fig. 12.2 Distributions of species in the 'pencil galaxias' species complex: Dwarf galaxias, *Galaxias divergens* (■); alpine galaxias, *Gl. paucispondylus* (■); bignose galaxias, *Gl. macronasus* (■). **Arrows** – ↑1: Hauraki Plains; ↑2: isolates in the west flowing upper Rangitikei River; ↑3: rivers of southern North Island, both along coastline north of Wellington and Ruamahanga River; ↑4: D'Urville Island and Marlborough Sounds; ↑5: Abel Tasman National Park in Tasman Bay; ↑6: absence from Aorere River and other Golden Bay catchments; ↑7: absence from Kahurangi National Park; ↑8: populations in the Buller River system; ↑9: range in West Coast rivers south to the Hokitika River; ↑10: absence from Clutha River; ↑11- ↑12: upper Waiau, Oreti and Mataura Rivers; ↑13: Lochy River, a tributary of Lake Wakatipu; ↑14: Manuhierikia River, Clutha River system; ↑15: upper Waitaki River in Mackenzie Basin; ↑16: upper Clarence and Wairau Rivers; ↑17: Maruia River headwaters, Buller River system; ↑18: absence from southern arm of Manawatu River; ↑19: Ngaruroro and Tukituki Rivers and northern branch of Manawatu River in southern Hawkes Bay; ↑20: absence in eastern North Island; ↑21: Rangitaiki River in Bay of Plenty

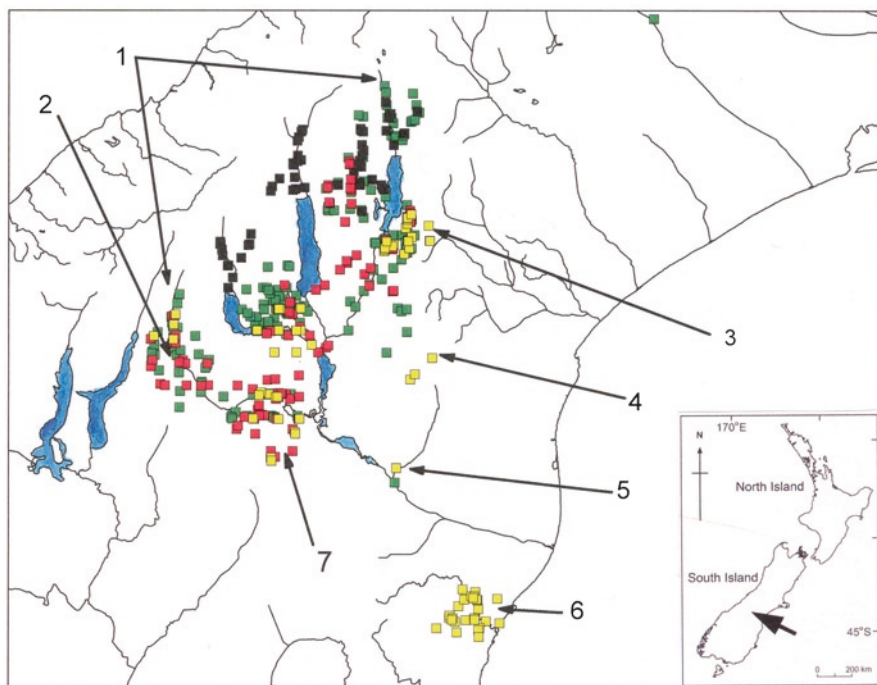


Fig. 12.3 Detailed distributions of members of the pencil galaxias species complex in the Mackenzie Basin and Kakanui River: Alpine galaxias, *Galaxias paucispondylus* (■); bignose galaxias, *Gl. macronasus* (■); lowland longjaw galaxias, *Gl. cobitinis*; (■); upland longjaw galaxias, *Gl. prognathus* (■). **Arrows** – ↑1: sites above the glacial lakes of the Mackenzie Basin; ↑2: upper Ahuriri River in the southern Mackenzie Basin; ↑3: Edward Stream below Burke's Pass; ↑4: upper Hakataramea River; ↑5: lower Hakataramea River in mid-Waitaki River; ↑6: Kauru and Kakanui Rivers; ↑7: Otematapaio River

species are found, with two of them being near-endemics (bignose galaxias entirely there – Figs. 12.2 and 12.3 – red symbols, and lowland longjaws spreading down into the mid-Waitaki, its mid/lower tributary the Hakataramea, and also into the nearby Kakanui River, a little further to the south – Figs. 12.3 and 12.4 – yellow symbols).

The distribution of this species complex, as a whole (Figs. 12.2–12.4), extends from the Hauraki Plains and Bay of Plenty, in the eastern/central North Island, south through the southern North Island, and across the northern, northwestern, and eastern South Island as far as some of the higher-level tributaries of the rivers of the Southland Plains (Waiau, Oreti and Mataura in the far south). Within this broad overall range, the various species have the following ranges:

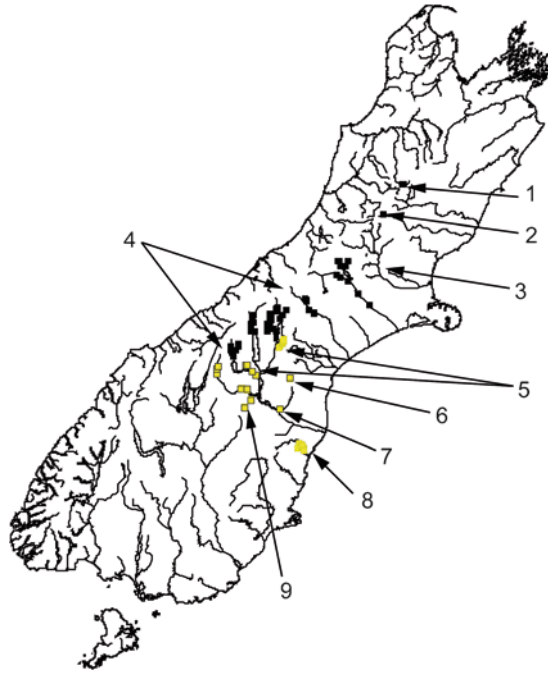


Fig. 12.4 Distributions of upland longjaw galaxias, *Galaxias prognathus* (■); and lowland longjaw galaxias, *Gl. cobitinis* (■). **Arrows** – ↑1: Maruia River, upper reaches of west flowing Buller River system; ↑2: upper Hurunui River; ↑3: absence from upper Waimakariri River; ↑4: Mackenzie Basin, upstream of glacial lakes; ↑5: Mackenzie Basin, upper Waitaki River system; ↑6: upper Hakataramea river, mid-reaches of Waitaki River system; ↑7: lower Hakataramea River; ↑8: Kauru and Kakanui Rivers; ↑9: Otamatapaio River

12.1 Dwarf Galaxias, *Galaxias divergens*, Mostly in Central New Zealand

Dwarf galaxias, *Gl. divergens*, is very widespread across central New Zealand (Fig. 12.2 – blue symbols). It is not found in far northern fresh waters, nor south across the western-central North Island, in the Waikato River/Lake Taupo/Tongariro River catchment, nor in Taranaki, the entire, large Whanganui River system and nearby catchments. The absence of dwarf galaxias widely across much of the western/central/eastern North Island is unlikely to be caused by a present lack of suitable habitats. However, much of the eastern central North Island was seriously impacted by the succession of major volcanic eruptions in the central North Island, and this area also has continuing geothermal/volcanic activity, which would certainly have affected fish populations in that area over many centuries (Wilson 1993; Wilson and Walker 1985; Wilson and Houghton 1993; McDowall 1996; Williams

and Keys 2008). There are rather disjunct populations in the headwaters of the Waihou River, Hauraki Plains (Fig. 12.2, arrow 1), and in upper tributaries of the Rangitaiki River, Bay of Plenty (Fig. 12.2, arrow 21). Recent results suggest that the Rangitaiki populations have disappeared, probably as a result of trout invasion – consistent with the findings of McDowall 2006). Dwarf galaxias is then absent from the eastern North Island (Fig. 12.2, arrow 20), until present in rivers of southern inland Hawkes Bay (Fig. 12.2, arrow 19).

To the south, from there, it is found in the lowermost tributaries, only, of the Ngaruroro River, in southern Hawkes Bay, and then is widely present in the Tukituki River just to the south of the Ngaruroro. Possibly its presence in the lower Ngaruroro signifies some earlier fluvial connections with the Tukituki. Further south again, dwarf galaxias is found widely in northeastern headwater tributaries of the Manawatu River (Fig. 12.2, arrow 18). The Ngaruroro, Tukituki and northern branches of the Manawatu River all drain the eastern flanks of the Kaweka, Kaimanawa and Ruahine Ranges of the central North Island. An interesting isolate is found in upper reaches of the Rangitikei River in the western slopes of the Ruahine Ranges (Fig. 12.2, arrow 2), and these populations are closest to populations from the Manawatu across on the eastern flanks of the Ruahine Ranges, both geographically and genetically (Waters et al. 2006). This association perhaps indicates some old fluvial connections or a headwater capture event across the mountain range, perhaps associated with the relatively recent (Pleistocene) uplift of these mountains (Kamp 1992a).

The presence of dwarf galaxias in the hill-country tributaries of the northern extremity of the northern arm of the Manawatu, and its absence from the southern arm of the Manawatu River except for its very southern extremities (Fig. 12.2, arrow 18), seems inexplicable, unless it is an outcome of the deep penetration of the Manawatu River system by alien brown trout, which certainly have seriously adverse impacts on fluvial galaxiids in most parts of New Zealand, and more widely (McDowall 2003, 2006). Or there could be other, unknown causes. Dwarf galaxias is also found in hill tributaries of the Ruamahanga River that drains the eastern flanks of the Tararua Ranges in the southern North Island. This rather erratic presence implies either local dispersal processes or local extirpation, possibly both. This area has a very complex Pleistocene geological history, including large areas of former marine environments (Kamp 1992a, b), but this seems long enough ago for dwarf galaxias to have had time to spread more widely among the modern river systems.

Dwarf galaxias also appears intermittently in several, other, well-separated southern North Island rivers, e.g., the headwaters of the Otaki and Waikanae River draining western slopes of the Tararua Ranges (but apparently not in the nearby Ohau River); then in the Wainuiomata and Hutt Rivers that drain southwards from the Rimutaka Ranges into Cook Strait in the southern North Island. Thus here, again, we find only intermittent presence of this species. These rather erratic patterns of presence/absence leave all sorts of unanswered questions about what influences the distribution of dwarf galaxias in the southern North Island, and there seems a fertile field for molecular studies and the connection of various galaxiid lineages to the geological history of the southern North Island. We need to bear in mind that the southern half of the North Island, about as far north as the present

volcanic plateau of the central North Island (Fleming 1979; Lewis and Carter 1994; Campbell and Hutching 2007), was submerged beneath sea as recently as the Pliocene, c. 5 Ma (see Fig. 3.3), so that any populations of dwarf galaxias present in the southern North Island must have invaded this area since it re-emerged from the sea. Dwarf galaxias could have spread from the northern South Island up the eastern flanks of the North Island mountain ranges, and if this is true, the rather disjunct and distinctly northern Waihou and Rangitaiki populations of dwarf galaxias must be viewed either as range extensions in terms of older history, or as relicts in the context of Central North Island volcanism, in which case they are 'recent relicts' if that is not a contradiction. Again, brown trout are highly invasive in this area, and their adverse impacts may be an explanation, but trout seem unlikely to have excluded the galaxiid so comprehensively across such a broad area and there would probably be some residual pockets remaining. Nothing further is known.

Dwarf galaxias is also widespread to the south of Cook Strait (Fig. 12.2, arrows 4–9), in the northern South Island. It is widely present in Marlborough (particularly Wairau, Clarence and Pelorus Rivers); in streams of the Marlborough Sounds and D'Urville Island (Fig. 12.2, arrow 4); also in the Nelson area, where it is found in the Motueka River, though only in its eastern tributaries – the Motueka and Motupiko – and not the western Wangapeka tributaries. It is present, too, in the small coastal streams draining east (into Tasman Bay) from Abel Tasman National Park: Fig. 12.2, arrow 5). It is noticeably absent, though, from the major rivers draining to the north and west into Golden Bay (such as the Takaka and Aorere: Fig. 12.2, arrow 6). It is absent, also, from west flowing rivers of the northwestern South Island from Farewell Spit, south and including those in Kahurangi National Park, rivers such as the Karamea and Heaphy (Fig. 12.2, arrow 7) (Jowett et al. 1998). It is thus absent from a substantial area of northern West Coast, South Island, drainages for reasons that are not obvious, though perhaps it is related to the absence of past or present fluvial connections with river systems further east where dwarf galaxias is widespread. This is an area that has had no significant human impacts. It was profoundly influenced by the bilateral displacement of landscapes to the east and west of the Alpine Fault (Soons 1992; Campbell and Hutching 2007; Bradshaw and Soons 2008), and so, possibly these northwestern catchments have not been accessible to dwarf galaxias since the northwestern South Island has reached its present position, and that this movement is reflected in the fish fauna (though there are upland bully and koura in these northwestern catchments and also occasionally brown mudfish, and it might have been expected that these populations would have been equally adversely affected – see discussion of the distribution of mudfishes in Chapter 14). Dwarf galaxias is then found widely, to the south, in several of the larger rivers of northern Westland, such as the Buller (Fig. 12.2, arrow 8), Grey, Taramakau and only as far south as the Hokitika River: Fig. 12.2, arrow 9); truncation of its southern range at the Hokitika River may be related to the presence, further south, of extensive ice sheets during the Pleistocene glaciations. Soons (1992) suggested that the most severe glaciation in Westland took place from about the town of Ross, southwards, and this is just to the south of the Hokitika River, providing a good match between the southern-

most range limits of dwarf galaxias and the more extensive impacts of Pleistocene glaciation (Main 1989; McDowall 1996).

There is what seems an unusually-sited dwarf galaxias population in a stream flowing into Lake Rotorua (Nelson Lakes); in general, non-diadromous fishes are only rarely present in lake tributaries (though see discussion, below, of others of this species group also found in lake tributaries). The Lake Rotorua population of dwarf galaxias presumably dates from before formation of the lake following glacial retreat, perhaps being a residual indicator of a former wider presence of this species in the upper Buller River that drains from these two headwater lakes.

Notably, also, dwarf galaxias is present in upper tributaries of the Maruia River, in the Buller River system (arrow 10), where several other *Galaxias* species are recorded as well, including upland longjaw galaxias, northern flathead galaxias of eastern South Island provenance (see below). In particular, the presence of dwarf galaxias in the upper reaches of the Maruia River (Fig. 12.2, arrow 17), where it co-occurs with upland longjaws and northern flathead galaxias, is of interest. Here, again, we see a species of northern and western provenance in the South Island (dwarf galaxias) co-occurring with one of southern and eastern provenance, and so clearly differing dispersal processes across the region.

Dwarf galaxias belongs to a group that generally tends to be sub-montane, and it is tempting to attribute its absence from some areas to its temperature preferences, and in particular that temperatures at low elevations might be too high for dwarf galaxias. However, this conclusion is not supported by this species' widespread presence in streams near sea level in the Marlborough Sounds and in Abel Tasman National Park (that are amongst the sunniest places in New Zealand – Fig. 12.2, arrows 4 and 5), and thus it is present in plenty of sites at low elevations, short distances inland, which are therefore unlikely to be very cool.

Waters et al. (2006) showed that dwarf galaxias is a sister lineage of alpine galaxias, and that these two lineages together form a sistergroup to bignose galaxias. This relationship might suggest that dwarf galaxias has southern origins, and escaped from the South Island into the North Island at a time of land connections across Cook Strait, perhaps in the Pleistocene. If so, it must then have spread rapidly north to reach the Bay of Plenty (Waihou and Rangitaiki Rivers (Fig. 12.2, arrows 1 and 21), as discussed previously in this chapter, though it was probably earlier. Waters et al. (2006) also provided a phylogram indicating relationships among a limited subset of populations of dwarf galaxias, in which Manawatu and Hutt River populations (southern North Island: Fig. 12.2, arrow 3), cluster closely together as a subgroup, but exhibit quite deep separation from populations from the northern South Island (Pelorus, Wairau and Motueka Rivers: Fig. 12.2, arrows 4 and 5), and all of these are deeply separated from rather more basal Buller River populations further south (Fig. 12.2, arrow 8). These relationships support a derivation of the southern North Island populations from those further south. Waters et al. (2006) also show that populations from the Pelorus River and the nearby Kaituna River, in the northeastern South Island form a sister clade to those from the Wairau, and that this is consistent with hypothesised different former river flow directions in the area from those at present – when the Kaituna and Pelorus Rivers connected south with the

Wairau, rather than both draining northwards to the sea in Pelorus Sound as they do now (Lauder 1970; Mortimer and Wopereis 1997; Craw et al. 2007).

There is an area in the range of dwarf galaxias that overlaps with alpine galaxias in the headwaters of the Wairau and Clarence Rivers of high-elevation inland Marlborough, northeastern South Island (Fig. 12.2, arrow 16). If dwarf and alpine galaxias are sister taxa, their sympatry probably implies differential redistributions of one or both species at some time (unless there was sympatric speciation), but even if there was differential redistribution, the species' overall ranges are substantially complementary, with dwarf galaxias primarily to the north/west and alpine galaxias to the south/east a probable instance of secondary sympatry.

The various pencil-galaxias lineages are found on both sides of the Southern Alps in the general area of the Lewis Pass and southwards (Fig. 12.2, arrow 17; 12.4, arrow 2), and a lineage split appears to be based here, with dwarf galaxias present largely to the west in headwaters of the Maruia River (upper Buller River system) and the sister lineage alpine galaxias to the east and south in the upper reaches of the Lewis River (Fig. 12.2, arrow 17). There is believed to have been a river capture event in which headwaters of the Lewis River were captured by the upper Maruia (Soons 1992; Craw et al. 2008), and the distributions of dwarf and alpine galaxias could reflect this as a possible vicariance event for the pencil-galaxias complex (McDowall 1970), even though this doesn't seem true of the *G. vulgaris* lineages (see Section 11.2.1).

12.2 Alpine Galaxias, *Galaxias paucispondylus*, Widely in the Eastern South Island

Alpine galaxias, *Gl. paucispondylus*, has a largely more southern/eastern range that is largely complementary to that of dwarf galaxias, being present only in the South Island and very largely east of the South Island mountain ranges. It is found mostly well inland in the intermontane river valleys, and typically in smaller tributary streams, often those draining the terraces alongside the main river channels (Fig. 12.2 – green symbols). There is an old (1965) record of alpine galaxias from the upper reaches of the Maruia River that has never been repeated and needs confirmation – it would be the only site known for alpine galaxias west of the Southern Alps. This Maruia record could, however, be a mis-identification made under the early misapprehension that only alpine galaxias has a white chevron in front of the dorsal fin (McDowall 1990, 2000) – Allibone (2002), based on genetic studies, has shown this chevron to be present also in some populations of dwarf galaxias. I therefore discount this old Maruia River record until it is re-confirmed by later corroboration.

Alpine galaxias is very widespread in the eastern South Island – from the Wairau and Clarence Rivers in the north, and then to the south in nearly all of the significant rivers draining the eastern flanks of the Southern Alps as far south as the Waitaki

(Fig 12.2 – green symbols). This includes presence both in the big intermontane valleys of the major braided rivers draining the higher alps (Waiau, Hurunui, Waimakariri, Rakaia, Rangitata, Waitaki), and also in the smaller ones draining the lower-elevation eastern foothills of the Southern Alps (such as the Ashburton, Opihi, and Orari – a marked contrast with the upland longjaw galaxias which is found in none of these smaller rivers – see below). Alpine galaxias in Canterbury rivers is typically well back into the intermontane valleys, and this may reflect temperature preferences. Occasional fish captured from rivers out on the Canterbury Plains may be expatriates carried downstream in river flows. There is no evidence for this species reproducing in the lower rivers, nor of a build-up of populations comparable with those in the higher-elevation, inland valleys.

Alpine galaxias is largely absent from the Clutha River system. There is a highly disjunct population in the headwaters of the Manuherikia River (Fig. 12.2, arrow 14), and this is the only population in the mid-lower Clutha – perhaps the Manuherikia population is an indicator of another river headwater capture involving the upper Manuherikia and the Ahuriri River (in the upper Waitaki River system and immediately to the north of the Manuherikia); the Ahuriri populations are by far the nearest conspecifics in a geographic sense, though they are in a completely separate river system. In fact the Manuherikia stock is the only one in the entire Clutha River system except for another outlier in the Lochy River, which now flows into the middle arm of Lake Wakatipu (Fig. 12.2, arrow 13).

The Lochy population of alpine galaxias implies presence of this species in the area prior to final formation of Lake Wakatipu – at which time the valley in which this arm of the lake is found drained southwards to join the Mataura River (Craw and Norris 2003). However, this does little to illuminate or clarify the otherwise peculiar absence of alpine galaxias from most of the Clutha River system (arrow 10), which begs explanation (and perhaps relates to the impacts of glaciation on the upper Clutha). Absence of alpine galaxias from the Kawarau River branch of the upper Clutha is consistent with the general absence, there, of all other non-diadromous fishes that are found elsewhere in the Clutha River system (see Section 11.2.7). Alpine galaxias is present in the rivers draining into the head of glacial Lake Tekapo (as are other non-migratory species, see Section 12.4). It seems that the Kawarau broke east out of a full Lake Wakatipu to eventually connect up with the mainstem Clutha River to the east, picking up the lower reaches of Bannock Burn as it joined the Clutha (see Fig. 11.5).

Further to the south of the Clutha, again, there is a series of alpine galaxias populations in various of the upper reaches of several of the south-flowing rivers of northwestern (inland) Southland – parts of the Waiau River, as in the Whitestone River, and in the Mararoa River, in tributaries upstream of the Mavora Lakes (Fig. 12.2, arrow 11); also in upper tributaries of the Oreti, a little further south and east (Fig. 12.2, arrow 12), and in the upper Mataura. Genetic studies comparable to those already undertaken of the *Galaxias vulgaris* species complex in the upper Waiau, Mataura and Oreti Rivers, and the integration of lineage distributions with the area's well-described geological history (Craw and Norris 2003) should prove informative.

12.3 Bignose Galaxias, *Galaxias macronasus*, a Mackenzie Basin Endemic

Bignose galaxias, *Gl. macronasus*, is probably a derivative of/shares a closest common ancestry with alpine galaxias, though if purely morphological characters were used to determine relationships, bignose may emerge as closer to dwarf galaxias. The c. 350 km separation between bignose populations in the Mackenzie Basin – Figs. 12.2 and 12.3 – red symbols), and the nearest populations of dwarf galaxias in rivers in the mountains of Marlborough (Fig. 12.2 – blue symbols, arrows 16 and 17), or in West Coast rivers (Fig. 12.2, arrow 8 and 9), may count against these species having a closer relationship, though it cannot be ignored. Though bignose galaxias was originally described from just two streams in the Mackenzie Basin near Twizel in the upper reaches of the Waitaki River, in the Mackenzie Basin (McDowall and Waters 2003) (Fig. 12.2, arrow 15), ongoing surveys, mostly by the Department of Conservation (Elkington and Charteris 2005; Bowie 2005; New Zealand Freshwater Fish Database) are revealing this species to be widespread across the Mackenzie Basin, from Edward Stream, just below Burke's Pass in the northeast (Fig. 12.3, arrow 3) south and west to the upper Ahuriri River valley, where it is widespread (Fig. 12.3, arrow 2). Despite their superficial morphological similarities, and their broadly overlapping ranges across the Mackenzie Basin (Fig. 12.3), alpine and bignose galaxias occupy distinctly different habitats, with alpine galaxias being found in larger, swift-flowing, coarse, shallow, cobble-substrate streams, whereas bignose galaxias tends to favour small, shingly creeks with finer substrates and more gentle flows, often those that drain, or are associated with small, perched wetlands and their associated spring streams; the two species may be found in sites only a few metres apart, but in very different habitats (Elkington and Charteris 2005; Bowie 2005).

12.4 Upland Longjaw Galaxias, *Galaxias prognathus*, only in the Large River Systems

Upland longjaw galaxias, *Gl. prognathus*, is widely, but intermittently, distributed along the eastern Southern Alps (Figs. 12.3 and 12.4 – black symbols), typically well up into the intermontane valleys, but only in tributaries of the larger rivers – the Hurunui (Fig. 12.4, arrow 2), Rakaia, Rangitata and Waitaki River systems. Waters and Craw (2008) speculate that the distribution of upland longjaws may be temperature limited – based on its presence only in the upper reaches of major, snow-fed river systems, the Rakaia, Rangitata and Waitaki, and they are probably right; this idea may have some interesting elements. Upland longjaws are often found in the small streams draining the shingly terraces along the flanks of the big snow-fed rivers, and these streams may be very cold, derived, as they often are, from ground water that probably has its origins in the snow-melt flows of the bigger rivers, themselves, or in springs

arising on the flanking, alluvial valley floors. Where found, upland longjaws are usually in coarse cobble/boulder habitats where flows are shallow, often with the upper substrate surfaces barely immersed in water.

Upland longjaw galaxias is notably absent from the Waimakariri River and (Fig. 12.4, arrow 3) and this seems inconsistent, particularly as other headwater galaxiids, such as Canterbury galaxias and alpine galaxias are present there. Nevertheless, there has been very widespread and intensive survey work in the upper river (e.g. McIntosh 2000 and New Zealand Freshwater Fish Database), and the species has not been found there. However, I always have an expectation that one day it may be found there, though dispersal is a chancy affair, and perhaps upland longjaws did fail to (re) penetrate this valley after the last retreat of Pleistocene glacial ice opened up the valley to invasion by freshwater fishes around 10,000 years ago. The cold temperatures of the glacial periods would have meant that cold-water habitats would have been available at much lower elevations than prevail today. Upland longjaws had to be in a 'position' to reinvade the intermontane valleys once retreat of the ice made habitats available, and perhaps they were not, in the Waimakariri.

Upland longjaw galaxias is also absent from all of the small to medium-sized rivers of Canterbury, such as the Waiau (North Canterbury), Waipara, Ashley, Selwyn, Ashburton, Hinds, Opihi, Orari, Waihao, Otaio, Makihikihi Rivers, in some of which alpine galaxias is widespread (compare Fig. 12.2 – green symbols for alpine galaxias, and Fig. 12.4 – black symbols for upland longjaw galaxias). This apparent absence could be because the uppermost, perhaps coldest, tributaries of these smaller rivers have not yet been sampled. There is an enigmatic population of upland longjaws in tributaries of the upper Maruia River (Fig. 12.4, arrow 1 – in the same Maruia tributary stream from which dwarf galaxias and northern flatheads have also been reported). There are no recent records of upland longjaws in the Maruia, despite several searches for the fish, but the species was once certainly present (I have seen specimens).

Upland longjaw is widely present in the Mackenzie Basin, notably upstream of the three major glacial lakes (Tekapo, Pukaki and Ohau) (Fig. 12.4 – black symbols, arrow 4), and this raises some interesting questions about how they reached these above-lake streams after glacial retreat. Upland longjaws were found in the upper Maruia, discussed earlier for northern flathead galaxias (see Chapter 11), close to where a headwater capture of a former Waiau River tributary has been identified (Soons 1992); however, so far, upland longjaw is not known anywhere in the upper Waiau, so there are some contradictions in the distributions of fishes here, and further search of the area is needed.

Presence of this species in the upper reaches of the Tekapo River in the Mackenzie Basin (part of the Waitaki River system) is of interest. Waters and Craw (2008) pointed out that the Tekapo River, rather than flowing south to join the Waitaki as it does now, formerly flowed east, joining with the Opuha River on its way to the east coast of the South Island; this was before the Tekapo River had been diverted further south and west by the uplift of the Two Thumb Range. This prompts the prospect that the upland longjaw might once have been present in the Opuha, though to date it has not been found there.

12.5 Lowland Longjaw Galaxias, *Galaxias cobitinis*, in the Waitaki and Kakanui Rivers

The lowland longjaw galaxias, *Gl. cobitinis* (Figs. 12.3 and 12.4 – yellow symbols), though described only recently (McDowall and Waters 2002), was long-known from a population in the Kauru River, a lower tributary of the Kakanui River (McDowall 1990), but was not distinguished from upland longjaw. The Kauru River population is at low elevations (50–70 m and <30 km upstream from the sea – Fig. 12.3 – yellow symbols, arrow 6; Fig. 12.4, arrow 8 – yellow symbols). The Kakanui River is close to, and may derive much of its flows via ground water from, the nearby, much bigger Waitaki River. Ongoing survey work in the Waitaki River, and particularly in the Mackenzie Basin, has revealed that this species is present there quite widely downstream of the upper Waitaki lakes (Tekapo, Pukaki, and Ohau – Fig. 12.3 – yellow symbols and Fig. 12.4, arrow 5 – yellow symbols; Elkington and Charteris 2005). It thus has a distribution there that is largely complementary to the upland longjaw. The low elevation Kauru/Kakanui populations of lowland longjaw (Fig. 12.4, arrow 8) could be a relict of the Pleistocene, when cold temperatures and advance of glacial ice may have driven freshwater fish populations to lower elevations on the forming Canterbury Plains, where this species may have once been more widespread? As temperatures ameliorated and ice retreated, populations may have retreated into the upper Waitaki, but there was nowhere in the Kauru for lowland longjaws to retreat to. It is possible that these populations of lowland longjaw at low elevations, as in the Kauru River, survive periods of summer-autumn low flows and their associated elevated water temperatures, by exploiting patches of cold ground-water upwelling into the stream channel; certainly, small shoals of larval/juvenile lowland longjaws can be found in such refuges (McDowall and Waters 2002).

There is a single, old (1980s), but unequivocal record of this species from the lower reaches of the Hakataramea River, a mid-Waitaki River tributary (Fig. 12.3, arrow 5; Fig. 12.4, arrow 7, yellow symbols) (there is a voucher specimen). However, several intensive searches at the original collection site have failed to find further fish of this species in the vicinity of the known previous collection locality, and this has caused some confusion. However, populations have recently been found in tributaries of the upper Hakataramea River (Fig. 12.3, arrow 4; Fig. 12.4, arrow 6 – yellow symbols), and the record from the lower river could have been based on an occasional expatriate fish derived from further upstream in the Hakataramea River.

Molecular examination of recently discovered populations of lowland longjaw in the upper Hakataramea show that these populations relate most closely to populations in tributaries of Edward Stream, an upper tributary of the Tekapo River in the Mackenzie Basin below (west of) Burke Pass (Waters and Craw 2008). These upper Hakataramea River and Edward Stream populations are separated, now, by a very long reach of river, involving the Tekapo joining the Waitaki, and the length of the

Waitaki downstream to the Hakataramea confluence, a distance of c. 189 km by river, though it is probably no more than 40 km by land. This much shorter distance by land between the upper Hakataramea and Edward Stream is seductive, prompting the prospect that there was once a more direct fluvial connection between the two groups of sites that could have involved a connection between the upper Hakataramea River and Edward Stream. The present saddle between Dalgety stream in the upper Hakataramea River and the Snow River which, like Edward Stream, joins Grays River, an upper Tekapo River tributary, is very low and some headwater capture between these streams seems not farfetched, perhaps involving uplift processes of the ranges of hills in the area – the Hunter, Dalgety and Grampian Mountains. Upland longjaw is not at present known from either Dalgety Stream or the Snow River, but the close proximity of these two streams, on both sides of a divide where lowland longjaw has been recorded, is a prospect that needs to be explored. Further sampling in these streams and molecular studies of other fish species present in both Dalgety Stream and the Snow River, such as alpine galaxias and upland bully, might help to clarify this question. It is of some relevance that alpine galaxias has been recorded from the Snow, suggesting that conditions suited to lowland longjaw galaxias may also be there. A confirmed absence from the Snow River would not be conclusive as it dewateres at times, and this would eliminate any fish populations that had been living there.

12.6 A Local Synthesis

Drawing these complex patterns together: The very wide distributions of the pencil-galaxias species group (Figs. 12.2–12.4) seems to suggest a quite old dispersal across the New Zealand landscape, though this species group's absence from Northland, and the Waikato-Taranaki-Whanganui-Manawatu areas in the western North Island (other than the occasional site in the Rangitikei River headwaters, mentioned above – Fig. 12.2, arrow 2), is distinctive and implies some dispersal processes different from other fish groups.

The contrast of alpine galaxias being widespread in most rivers of Canterbury, and also in north Otago and Southland: Fig. 12.2 – green symbols), but upland longjaw galaxias being much more restricted and present only in the Hurunui, Rakaia, Rangitata and Waitaki Rivers, that drain the eastern flanks of the Southern Alps: Fig. 12.4 – black symbols, arrows 2–4) is striking but has no obvious explanation. It seems unlikely to be due to the lack of enduring suitable habitat conditions, as the two species often co-occur. It is all the more curious, given that upland longjaw has also been found in the west-flowing upper Maruia River, whose source population is unknown (Fig. 12.4, arrow 1), which it shares with dwarf galaxias (as well as northern flathead galaxias). Thus parts of the range of upland longjaw galaxias look relictual but an explanation is elusive, but as discussed for northern flathead galaxias (see Section 11.2.1), this area was probably heavily impacted over a long period

by Pleistocene glaciation, and the distributions of fish in the area may result from invasion/recovery after glacial conditions ameliorated.

The modest diversity of this species group in the Mackenzie Basin, with four species there (Figs. 12.2–12.4) is distinctive in the context of the distributions of other non-diadromous freshwater fish groups. It includes two quite widespread pencil-galaxias species (alpine galaxias and upland longjaw galaxias), and two near basin endemics – bignose galaxias found only in the Mackenzie Basin and lowland longjaws also found downstream from the Mackenzie Basin in two Waitaki tributaries (Otamatapaio – Fig. 12.3, arrow 7 and 12.4, arrow 9, and Hakataramea, arrows 4 and 5, all yellow symbols) and in the nearby Kakanui River (the Kauru tributary, arrow 6). The large number of sites indicated in Fig. 12.3 at arrow 6 reflects intense surveys for this critically endangered species (the stream involved is heavily abstracted for pastoral irrigation).

How old this small radiation is, is unknown, but it could be quite ancient. It is possible that parts of the Mackenzie basin were implicated in the residual southern South Island that remained as emergent land during the Oligocene drowning of much of New Zealand (if there was any emergent land – Landis et al. 2008), making it conceivable that the pencil galaxias complex dates that far back in New Zealand's biogeographical history: it had to come from somewhere! The map of residual New Zealand at that time published by Cooper and Cooper (1995) seems to include this southern hypothetical island extending as far as the vicinity of the Mackenzie Basin, and the origins of the pencil galaxias complex in the area could be illuminated by molecular studies. If the greatest diversity of the pencil galaxias complex is indicative of its origins in the Mackenzie Basin, it appears as though the group has spread northwards, moving well into the North Island (dwarf galaxias) presumably when there were land connections across the present Cook Strait and north as far as the Bay of Plenty at least prior to the major North Island volcanism (see Section 3.5).

References

- Allibone RM (2002) Dealing with diversity dwarf galaxias style. *Water Atmos* 10(1):18–19
- Bowie S (2005) Bignose galaxias (*Galaxias macronasus*) survey in the Mackenzie Basin. Canterbury, Department of Conservation, Twizel, N Z, 36 pp
- Bradshaw M, Soons J (2008) The lie of the land. In: Winterbourn MJ, Knox GA, Burrows C, Marsden I (eds) *The natural history of Canterbury*. Canterbury University Press, Christchurch, N Z, pp 15–36
- Campbell HJ, Hutching G (2007) *In search of ancient New Zealand*. Penguin, Auckland, N Z, 238 pp
- Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Trends Ecol Evol* 261:293–302
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend CR (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 17–34

- Craw D, Anderson L, Rieser U, Waters JM (2007) Drainage reorientation in Marlborough Sounds, New Zealand, during the Last Interglacial. *N Z J Geol Geophys* 50:13–20
- Craw D, Burridge CP, Norris R, Waters JM (2008) Genetic ages for Quaternary topographic evolution: a new dating tool. *Geology* 36:19–22
- Elkington SP, Charteris SC (2005) Freshwater fish of the upper Waitaki River. Department of Conservation, Christchurch, N Z, 44 pp
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp
- Jowett IG, Hayes JW, Deans N, Eldon GA (1998) Comparisons of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. *N Z J Mar Freshwat Res* 32:307–322
- Kamp PJJ (1992a) Landforms of Hawke's Bay and their origin: a plate tectonic interpretation. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 344–366
- Kamp PJJ (1992b) Landforms of Wairarapa: a geological perspective. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 367–381
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Lauder WR (1970) The ancient drainages of the Marlborough Sounds. *N Z J Geol Geophys* 13:747–749
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea conference, Christchurch, New Zealand, 27–30 November, 1992. Balkema, Rotterdam, The Netherlands, pp 119–137
- Main MR (1989) Distribution and post-glacial dispersal of freshwater fishes in South Westland, New Zealand. *J R Soc N Z* 19:161–169
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool, Harv Univ* 139:341–431
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1996) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (2000) Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 224 pp
- McDowall RM (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Trans Am Fish Soc* 132:229–238
- McDowall RM (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool temperate galaxioid fishes. *Rev Fish Biol Fisher* 16:233–422
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. *N Z J Zool* 29:41–52
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. *J R Soc N Z* 33:675–691
- McIntosh AR (2000) Habitat and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Can J Fish Aquat Sci* 57:2140–2151
- Mortimer N, Wopereis P (1997) Change in direction of the Pelorus River, Marlborough, New Zealand: evidence from composition of Quaternary gravels. *N Z J Geol Geophys* 40:307–313
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 439–455

- Waters JM, Crow D (2008) Evolution and biogeography of New Zealand's longjaw galaxiids (Osmeriformes: Galaxiidae): the genetic effects of glaciation and mountain building. *Freshwater Biol* 53:521–534
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid fish lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Williams K, Keys H (2008) Ruapehu erupts. Godwit, Auckland, N Z, 63 pp
- Wilson CJN (1993) Stratigraphy, styles and dynamics of lake Quaternary eruptions from Taupo volcano, New Zealand, *Phil Trans R Soc Lond A* 343:205–306
- Wilson CJN, Houghton BF (1993) The Taupo eruption. Institute of Geological and Nuclear Sciences, Taupo, N Z, 6 pp
- Wilson CJN, Walker GPL (1985) The Taupo eruption, New Zealand. 1. General aspects. *Phil Trans R Soc Lond A* 314:199–228

Chapter 13

Pattern and Process in the Distributions of Non-diadromous Species 3:

The Dune Lakes Galaxias

Abstract The dune lakes galaxias is a non-diadromous, lacustrine derivative of the inanga, *Galaxias maculatus*, and is found only in a few small lakes in northern New Zealand; relationships of the various lake populations to inanga seem complex and may not result from a single speciation event.

Keywords Derivations • Dune lakes galaxias • Inanga • Northland • Relationships

13.1 Dune Lakes Galaxias, *Galaxias gracilis*, a Lacustrine Stock in Northern New Zealand

The dune lakes galaxias, *Galaxias gracilis* (Fig. 13.1), is a small, non-diadromous, entirely lacustrine, mid-water, shoaling species that is distinctive in the New Zealand context on account of these behavioural attributes. It is found only in a series of small lakes in western Northland (Fig. 13.2) – the Kai Iwi Lakes north of Dargaville (Fig. 13.2, arrow 4 – red symbols), Lake Rototuna (Fig. 13.2, arrow 5), and the Poutu Lakes, about 16 km further to the south on the north head of the Kaipara Harbour (Fig. 13.2, arrow 7). (A population of this species in Lake Ototoa, on the South Kaipara Head (Fig. 13.2, arrow 8) is the result of known human translocation of stocks from Lake Humuhumu, one of the Poutu Lakes to the north; Thompson 1989); this release was made ostensibly to provide a forage fish for rainbow trout (*Oncorhynchus mykiss*) that are stocked in the lake. Its survival in Lake Ototoa under predation of rainbow trout is surprising given the known seriously adverse impacts of trout predation on this species in other lakes (Fish 1966; Cudby and Ewing 1968, Cudby et al. 1969; Allen et al. 1971; McDowall 2006), though its current status in the lake may be further threatened by the illicit liberation of another predator, European perch, *Perca fluviatilis* (f. Percidae) in the lake. The dune lakes galaxias is viewed as a landlocked derivative of the diadromous inanga (McDowall 1967, 1970; Ling et al. 2001). The lakes involved have no significant streams associated with them, either streams bringing water into the lakes, or streams discharging it from them.

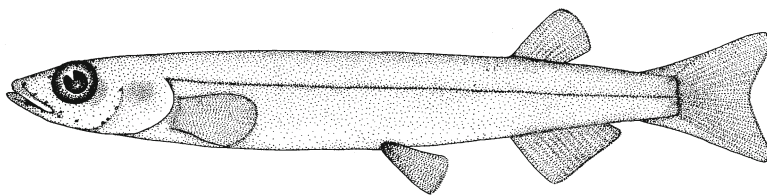


Fig. 13.1 Dune lakes galaxias, *Galaxias gracilis*, 59 mm LCF (family Galaxiidae)

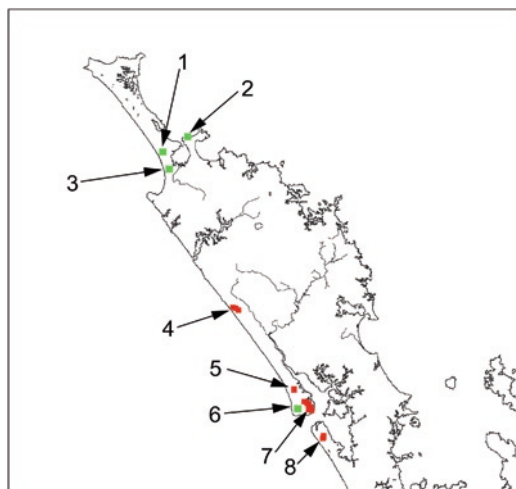


Fig. 13.2 Distribution of dune lakes galaxias, *Galaxias gracilis* (■), and lake-limited populations of inanga, *G. maculatus* (■) in Northland. **Arrows** – ↑1: Lake Waiparera; ↑2: Lake Ohia; ↑3: Lake Ngatu; ↑4: Kai Iwi Lakes; ↑5: Lake Rototuna; ↑6: Lake Mokeno; ↑7: Poutu Lakes on north head of Kaipara Harbour; ↑8: Lake Ototoa, a translocated population

There is some uncertainty about the derivations and relationships of the various populations included in the dune lakes galaxias (McDowall 1972, 1990, 2000). Some molecular evidence suggests that the populations included in the species *Gl. gracilis* may have dual or even multiple derivations from the diadromous inanga (Ling et al. 2001). The New Zealand Department of Conservation treats the Kai Iwi and North Kaipara (Poutu) lakes groups of populations as two separate lineages for conservation management purposes (Allibone and Barrier 2004), though the Kai Iwi Lakes populations have not been formally described. Some of the results of genetic studies seem at best inconsistent. Ling et al. (2001), for instance, presented cluster analyses of dune lakes galaxias along with a series of landlocked populations of inanga (from which dune lakes galaxias is probably derived) using three datasets:

1. Morphometric data
2. Meristic data
3. Molecular data (Fig. 13.3)

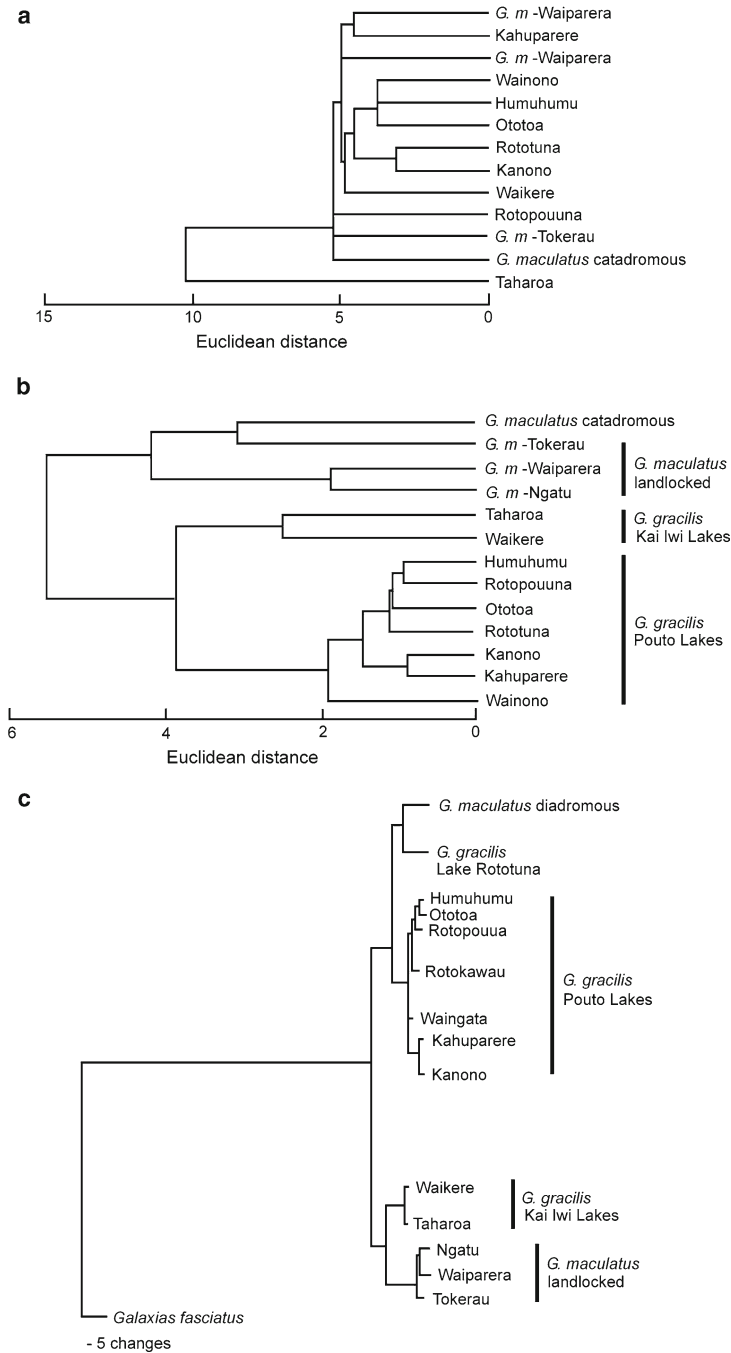


Fig. 13.3 Hypothesised relationships among populations of dune lakes galaxias, *G. gracilis*, and diadromous and landlocked populations of inanga, *G. maculatus*, based on **a**: Morphometric data; **b**: Meristic data; and **c**: molecular data derived from D-loop sequence (adapted from Ling et al., 2001)

The morphometric data group all but one of the studied populations as a sister clade to just one of the Kai Iwi lakes' populations (L. Taharoa), with a diadromous population of inanga within the cladogram rather than sister-taxon to the rest (Fig. 13.3).

However, meristic data from a series of landlocked populations of inanga group them with diadromous inanga populations (Fig. 13.3b), and these form a sister clade to all of the populations treated as *Gl. gracilis*, in McDowall (1972, 1990). Moreover, the branches cluster populations according to geography – grouping populations in the Kai Iwi Lakes (Fig. 13.2, arrow 4), separately from those on the North Kaipara head (arrows 5 and 7). Meristic characters are known to be labile and vulnerable to the impacts of environmental influences during early ontogeny. In particular, in lower euteleosts like galaxiids, water temperatures and salinities during egg development are known to affect the numbers of serially repeated body parts like vertebral number (McDowall 1972, 2004). For this reason, little weight can be assigned to the phylogenetic significance of variation in such characters, or groups based on them.

Molecular data (Fig. 13.3), however, tell a different story. They group most of the populations from the North Kaipara Head together, except for the population in Lake Rototuna. The latter is grouped in a separate clade, together with diadromous *Gl. maculatus*, and these form the sister clade to all of the other North Kaipara populations. All of these populations, diadromous or not, are sister, in turn, to another clade in which there are two sub-clades, one comprising the populations from the Kai Iwi Lakes, whereas the other clade comprises three Northland landlocked populations of inanga.

Later genetic results added a landlocked population of inanga from Lake Mokeno (which is in close proximity to the lakes on North Kaipara Head – Fig. 13.2, arrow 6 – green symbols) to the clade including three landlocked populations of inanga from northeastern Northland (Fig. 13.2, arrows 1–3 – green symbols). The latter three populations are a long distance (c. 150 km) from the lakes on the North Kaipara, and altogether, these results pose a series of complex taxonomic issues.

In particular:

1. The sister-clade association of diadromous inanga with just one of the seven dune lakes populations (that in Lake Rototuna), to the exclusion of all the others, makes little phylogenetic sense, even though the Lake Rototuna populations is a modest distance (c. 10 km) from the other North Kaipara lakes, which are in closer proximity to each other.
2. The greater genetic separation of the North Kaipara populations from the Kai Iwi Lakes populations seems sensible (they are c. 40 km apart).
3. The wide genetic separation of the diadromous populations of inanga from the landlocked lake inanga populations is also of dubious likelihood, as each of the populations in the latter lakes is almost certainly independently derived from diadromous stocks.
4. Also, separate derivation of each of the three lake inanga populations from diadromous stocks seems probable, just on geographic grounds and it is hard to

imagine that these three small dune lakes were ever connected by fresh water (Ngatu and Waiparera are c. 10 km apart and Tokerau Lagoon is c. 15 km from Waiparera). The three populations in these lakes seem likely to have independent derivations from diadromous inanga populations and adding Lake Mokeno to the scenario (which is c. 150 km distant) just adds to the controversy – it seems quite inconceivable that Lake Mokeno (Fig. 13.2, arrow 6) was in any way implicated in this pattern of derivations of the landlocked populations.

5. The close association of these landlocked inanga with the Kai Iwi Lakes populations of dune lakes galaxias also makes little sense, especially given their wide geographical separation; it seems totally unlikely that there were ever any freshwater connections between the lakes having landlocked inanga and the Kai Iwi Lakes.

So, together, all of the connections implied by genetic data seem biogeographically inconsistent and further molecular studies are needed before a clear picture of derivations and relationships can be achieved.

Rowe and Chisnall (1995, 1997) addressed the distribution of dune lakes galaxias populations in the context of the ages of the several lakes involved, and explored how this distribution could have been achieved, given their spread across an 80 km length of coastline – and, recognising the low likelihood that these various lakes, themselves, were ever connected by water. The populations of dune lakes galaxias seem to comprise one or more non-diadromous isolates of the diadromous inanga, and their distributions probably reflect geographically isolated processes. These are interesting questions for future studies, but clarifying them is not crucial to obtaining a broad understanding of the patterns and processes of the biogeography of the fauna.

Rowe and Chisnall (1997) suggested that the series of lakes where the dune lakes galaxias is found comprise those that are more distant from the existing western sea shore of Northland. They reported that these groups of lakes vary greatly in age, some of them being Pleistocene while others are mid to late Holocene, and the populations of dune lakes galaxias are present in the older series of lakes. They speculated about the possibility of human translocation in New Zealand's pre-European history – though there are no known/recorded traditions of such translocations by Maori in relation to these lakes. Moreover, the fish themselves are so small (usually less than c. 65 mm), that they are unlikely to have attracted much interest as a dietary item for the Maori people of the district; this makes Maori translocations seem unlikely.

References

- Allen PJ, Turner DLP, Little RW (1971) Survey of Kai Iwi Lakes. N Z Mar Dep, Freshwater Fisheries Advisory Service, Invest Rep (North Island) 6:1–1
- Allibone RM, Barrier RFG (2004) New Zealand non-migratory galaxiid fishes recovery plan, 2003–2013. N Z Dep Cons Threatened Spec Rec Plan 53:1–45

- Cudby EJ, Ewing NB (1968) Lakes Taharoa and Kai Iwi, Northland. Unpublished report, Fisheries Management Division, Marine Department, Wellington N Z, 5 pp
- Cudby EJ, Ewing NB, Wilkinson R (1969) Lakes Taharoa and Kai Iwi, Northland, Unpublished report, Fisheries Management Division, Marine Department, Wellington N Z, 6 pp
- Fish GR (1966) An artificially maintained trout population in a Northland lake. N Z J Sci 9:200–210
- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species; the ‘new’ biodiversity and evolutionary significant units among New Zealand’s galaxiid fishes. J Fish Biol 59(Suppl A):209–222
- McDowall RM (1967) New landlocked fish species of the genus *Galaxias* from North Auckland, New Zealand. Breviora 265:1–11
- McDowall RM (1970) The galaxiid fishes of New Zealand. Bull Mus Comp Zool Harv Univ 139:341–431
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). J R Soc N Z 2:325–367
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (2000) Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 224 pp
- McDowall RM (2004) Variation in vertebral number in galaxiid fishes, how fish swim, and a possible reason for pleomerism. Rev Fish Biol Fish 13:247–263
- McDowall RM (2006) Crying wolf, crying foul, crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes. Rev Fish Biol Fish 16:233–422
- Rowe DK, Chisnall BL (1995) Conservation status of dwarf inanga (*Galaxias gracilis*) and recommendations for its future management. NIWA Sci Tech Ser 24:1–55
- Rowe DK, Chisnall BL (1997) Distribution and conservation status of the dwarf inanga *Galaxias gracilis* (Teleostei: Galaxiidae) an endemic fish of Northland dune lakes. J R Soc N Z 27:229–233
- Thompson FV (1989) Dwarf inanga successfully introduced to Lake Ototoa. Freshwater Catch (N Z) 39:13

Chapter 14

Distribution, History and Biogeography of the *Neochanna* Mudfishes

Abstract Five species of *Neochanna* mudfish are nondiadromous derivatives of the diadromous Tasmanian mudfish. The New Zealand species are widespread from far Northland to the eastern central South Island. They are in general allopatric, though two species are found in close proximity in northern latitudes. They are all found in wetlands, often in debris-filled habitats and have distinctive specialisations that adapt them to living in such places. They are capable of aestivation when aquatic habitats dry up. Brown mudfish is present on both sides of Cook Strait, probably a direct consequence of land connections across the strait at times of lowered sea levels in the Pleistocene. Absence of brown mudfish from South Westland reflects Pleistocene glaciation there. A mudfish species on the Chatham Islands, east of mainland New Zealand, is the only non-diadromous species on the island, and its presence there must post-date the emergence of the islands from marine submergence, believed to have been late in the Cenozoic.

Keywords Aestivation • Chatham Islands • Land bridges • Mudfishes • *Neochanna* • Pleistocene

14.1 A Radiation of *Neochanna* Mudfishes in Australia and New Zealand

The *Neochanna* mudfishes form a distinctive clade of small (to 180 mm), slender, cigar-shaped, flexible-bodied species (Figs. 14.1 and 14.2) that exhibit explicit adaptations for life in debris-filled wetlands and spring heads, where water flow may be ephemeral, often pools in the forest. They tend not to co-exist with other fish species (Eldon 1978, 1979a), and it seems that this has dual implications/causations. In part it is that mudfishes are able to persist in habitats where the presence of free water is ephemeral, in a way that other fish cannot, and in part it is that mudfishes do not seem to be able to cope with the predation pressures and/or competition with other species. They have small eyes and large, tubular, anterior nostrils that project well forward above the upper lip; the pelvic fins are often

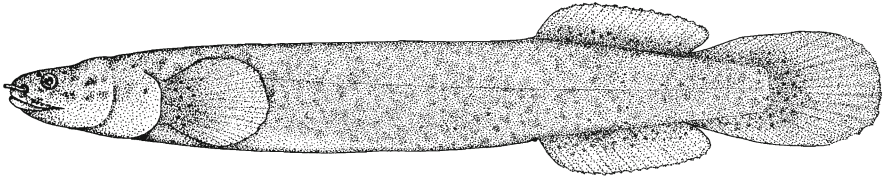


Fig. 14.1 Burgundy mudfish, *Neochanna heleioides*, 92 mm TL (family Galaxiidae), a localised northern endemic

Fig. 14.2 An aestivating brown mudfish, *Neochanna apoda* (photo: G.A. Eldon)



reduced in size, or the pelvic girdle and fins are absent altogether, and they have the posterior of the body with the dorsal, caudal and anal fins conjoined to provide strong propulsion through debris in habitats occupied. The caudal fin itself is strongly rounded in shape. The cranial osteology of the mudfishes is also modified in ways that are interpreted as strengthening the anterior of the cranium (McDowall 1997), and this too is probably related to their use of weed-crowded and debris-filled habitats through which they move, at times. They can respire through the skin (Meredith et al. 1982) and this gives them the ability to survive by aestivating in damp substrate refuges when free water disappears from their habitat (Eldon 1968, 1978, 1979a, b; Eldon et al. 1978; McDowall 1990; O'Brien and Dunn

2005, 2007). It is often assumed that mudfish are tolerant of low oxygen levels in the water, but this seems untrue (Eldon 1978, 1979b; Eldon et al. 1978); when oxygen levels in their habitat become stressful, mudfish may be found ‘hanging’ at the surface of the water, gulping air (McDowall 1999; Meredith et al. 1982), and they are capable of absorbing oxygen through the skin and presumably the oral epithelium.

The phylogenetic relationships among the six mudfish species, based on both morphological and molecular data, and including the one species that is present in both Tasmania and southern Victoria and five in New Zealand, are indicated in Fig. 7.4 (McDowall 2004; Waters and McDowall 2005). These suggest that the Australian species is the sister taxon of all five New Zealand species, thus requiring only a single derivation of the latter from the Australian form. The fact that the Australian species is amphidromous, with marine-living larvae and juveniles (Fulton 1986) provides an obvious potential mechanism for the derivation of the New Zealand *Neochanna* by transoceanic dispersal from Tasmania across the Tasman Sea in the southwestern Pacific. As discussed earlier, the derivations of the New Zealand species seems too recent to involve ancient, late Cretaceous Gondwanan connections (Waters and White 1997; Waters and McDowall 2005).

None of the New Zealand species of *Neochanna* now has a marine-living juvenile, and when, and how often, this life stage was lost subsequent to the likely dispersal of the ancestral *Neochanna* lineage to New Zealand, is unknown. It might seem parsimonious to assume a single loss – though other evidence suggests that this conclusion may be only superficially parsimonious. Of much relevance to these questions is the likelihood that the Chatham Islands may have only relatively recently emerged above the sea, perhaps only about 2–3 million years ago (Campbell et al. 1993, 2009; Campbell and Hutching 2007). This raises major questions as to the derivation of the Chatham species of *Neochanna* that remain unanswered, but dispersal seems implicated, and it must have been if Campbell and his colleagues are right about the relatively recent (in geological terms) emergence of the islands from the sea. The apparently basal, or near-basal, position of the Chatham mudfish (see Fig. 7.4) (McDowall 2004; Waters and McDowall 2005) among the New Zealand *Neochanna* species, both morphologically and genetically, suggests that it may have been present in the Chatham Islands for about as long as there have been mudfishes on mainland New Zealand, but this rather conflicts with the idea that the Chatham Islands have been submerged by seas, i.e. the Chatham mudfish must have arrived there since the islands re-emerged, and freshwater habitats became available there, and presumably must have been diadromous to do so. Thus, the retention of a marine life stage, at least in the Canterbury mudfish to late Pliocene or Pleistocene times, would then seem to have been necessary.

The presence of a well-developed pelvic girdle and associated fins in the Chatham species implies its quite basal position among the various New Zealand mudfishes (unless restoration of the fins took place, which is, I suppose, not

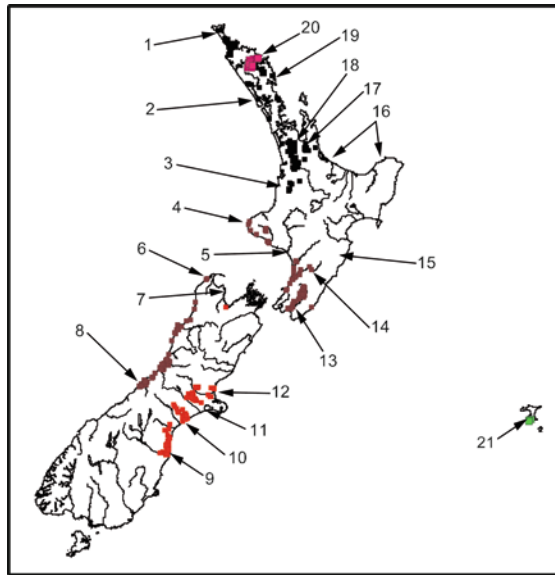


Fig. 14.3 Distributions of the *Neochanna* mudfishes: black mudfish, *N. diversus* (■); burgundy mudfish, *N. heleioides* (■); brown mudfish, *N. apoda* (■); Canterbury mudfish, *N. burrowsius* (■); Chatham mudfish, *N. rekohua* (■). **Arrows** – ↑1: former island at north of Aupouri Peninsula; ↑2: record on the north head of Kaipara Harbour; ↑3: southern limits of black mudfish at Mokau River; ↑4: populations west of Mount Taranaki; ↑5: absence from Wanganui River; ↑6: site near Whanganui Inlet; ↑7: absence from Tasman and Golden Bays; ↑8: southern limits at Okarito; ↑9: south to south bank of Waitaki River; ↑10: south of Rakaia River; ↑11: north of Rakaia River; ↑12: Oxford in North Canterbury; ↑13: Ruamahanga River; ↑14: sites in Manawatu River just west and just east of Manawatu Gorge; ↑15: absence from southern Hawkes Bay and northern Wairarapa; ↑16: absence from Bay of Plenty and eastern North Islands; ↑17: Hauraki Plains and lower Waikato; ↑18: lower Waikato River sites; ↑19: site south towards Auckland Isthmus; ↑20: distribution of burgundy mudfish within that of black mudfish; ↑21: Chatham mudfish, *N. rekohua*

impossible, though it seems unlikely. Reduction and loss of the pelvic fins in most of the mudfish species is probably related to the damage they would suffer when pushing through habitat debris, and I have seen specimens of the Chatham species with pelvic fins reduced to shredded stubs. So, taking a broad view of derivations and relationships, there are some complications for which an explanation does not seem obvious, especially the quite basal position of the Chatham Island species. Waters and White (1997) suggest the Pliocene as the age of mudfishes in New Zealand, which seems relatively recent, but provides something of a temporal framework for interpreting the origins and radiation of the New Zealand species.

The distributions of the various mudfish species across mainland New Zealand are less perplexing (see Fig. 14.3).

14.2 Black Mudfish *Neochanna diversus* in Northern New Zealand

The black mudfish (Fig. 14.3 – black symbols), *N. diversus*, is found widely in northern New Zealand, from a little south of North Cape (Fig. 14.3, arrow 1), south to the lower Waikato River system (Fig. 14.3, arrow 18), with additional populations further south again, in the headwaters of the west-flowing Mokau River (Fig. 14.3, arrow 3 – black symbols). This species has recently been recorded, for the first time, from the vicinity of the Auckland Isthmus (Fig. 14.3, arrow 19); its presence in that area is unsurprising, apart from the very intensive human development associated with New Zealand's largest city. There are populations also to the east in the Hauraki Plains (Fig. 14.3, arrow 17). but it seems that this species is absent from the fresh waters of the Bay of Plenty further to the east of the Hauraki Plains (and thus east of the Kaimai Ranges) (Fig. 14.3, arrow 16). Absence of any mudfish in catchments of the Bay of Plenty is not inconsistent with central North Island volcanism (McDowall 1996), and as discussed elsewhere for dwarf galaxias (Chapter 13) and Cran's bully (Chapter 15). It could, perhaps, have once been present in the Bay of Plenty and have been extirpated there, though there is no explicit indication of this.

An interesting and presently unresolved question relates to origins of the farthest northern distribution of black mudfish. The population in wetlands near Parengarenga Harbour a little south of North Cape/Cape Reinga (Fig. 14.3, arrow 1) is around 30 km further north than the nearest other known sites on the Aupouri Peninsula of Northland, a little further south (see Fig. 3.3). The far north landscape of Northland was reputedly once a small island unconnected to the rest of the North Island, until connection was established by formation of a sand spit (tombolo) during the Pleistocene (Brook 1999). An interesting question that needs to be addressed relates to whether the most northern (Parengarenga) population of black mudfish invaded the far north as or after the sand spit was formed, or whether it was present on the far northern, once isolated, island before formation of the connecting sand spit. Further molecular studies are needed.

Gleeson et al. (1999) described DNA sequence divergence between Northland and Waikato populations of black mudfish, and attributed this to historic separation of these two areas by the Manukau Strait, a former Pliocene sea-way across what is now the Auckland Isthmus, but they didn't attempt to establish a chronology for these geological events in relationship to patterns suggested by the molecular data.

14.3 Burgundy Mudfish, *Neochanna heleioides*, a Localised Northland Endemic

The burgundy mudfish, *N. heleioides*, occupies a relatively small area of Northland, inland from Kerikeri, in the Bay of Islands, including the vicinity of Lake Omapere (Fig. 14.3, arrow 20 – purple symbols). This is an area within, and in close proximity

to, parts of the surrounding range of the black mudfish. Ling and Gleeson (2001) suggested that the burgundy mudfish is restricted to the Kerikeri volcanic plateau at elevations around 200 m, but more recent discoveries show that it is rather more widespread than that (Fig. 14.3 – purple symbols). The narrow range of burgundy mudfish perhaps has the appearance of this species being a refugial survivor whose distribution was enveloped by black mudfish – the two northern mudfishes seem to have allopatric distributions and there are no records of them co-occurring, though should this occur it might not be noticed unless specimens were examined with care. Studies of relationships, both morphological and molecular (Gleeson et al. 1999; Ling et al. 2001; McDowall 2004; Waters and McDowall 2005) suggest that the closest affinities of burgundy mudfish may lie with brown mudfish, found well to the south (Fig. 14.3 – brown symbols, arrows 4–8), rather than with the geographically much closer black mudfish. This, too, raises complex historical biogeographical questions that seem to elude easy explanation.

14.4 Brown Mudfish, *Neochanna apoda*, Widespread in Central New Zealand

The brown mudfish, *N. apoda*, is found widely across the southern North Island and the northwestern South Island (Fig. 14.3 – brown symbols). The area to the west of Mount Taranaki, where the most northerly populations of brown mudfish are found (Fig. 14.3, arrow 4) would have been intensively influenced by enduring to relatively-recent substantial volcanism of Mount Taranaki (the most recent eruption was only c. 300 years ago – Neall 1992). The far northern range limits of brown mudfish are near Cape Egmont just west of Mount Taranaki (Fig 14.3, arrow 4), and the biogeography of the separation of the northernmost brown mudfish populations in central Taranaki, from the southernmost populations of black mudfish further north (south as far as the headwaters of the Mokau River catchment: Fig. 14.3, arrow 3 – black symbols) is uncertain – though the range limits of the two species are now well separated.

What creates the northwestern/inland limits of brown mudfish is not obvious, but the pattern could be a residue of former central (Taupo) and western (Mt Taranaki) North Island volcanism (though the populations are well to the west of the areas of greatest impacts of the Taupo eruptions). Brown mudfish extends south, widely through the western and southern North Island, but there is a quite wide range gap between the Patea and Rangitikei Rivers, including the apparent lack of mudfish from the entire, extensive Whanganui River system, an absence that is enigmatic (Fig. 14.3, arrow 5). It could relate to massive floods of once ash-filled river basins following the AD 186 Taupo eruption, and a failure of the fish to re-invade the area, but this issue remains highly unresolved. Brown mudfish is now present in wetlands along the coastline to the north of Wellington, though the populations are sporadic in occurrence and near relictual in places owing to extensive wetland drainage for pastoral farming and, in most recent decades, intensive human settlement.

In the Wairarapa area, to the east of the southern North Island mountain ranges (Ruahines, Tararuas and Rimutakas), brown mudfish is primarily found only in the

south-flowing Ruamahanga River (Fig. 14.3, arrow 13), being generally absent from both northern and southern Wairarapa tributaries of the Manawatu River (Fig. 14.3, arrow 14). This presence in the Ruamahanga but absence from the southern branch of the Manawatu defies obvious explanation, unless presence in the Ruamahanga River area relates to formerly more westerly drainages in the southern North Island disrupted by uplift of the Rimutaka Ranges in the southern North Island, and it is clear that this area has a complex geological history (Kamp 1992; Eyles and McConchie 1992). There is parallel general absence of dwarf galaxias from the southern arm of the upper Manawatu River. A very old (1939) newspaper record of brown mudfish from a site a little east of the Manawatu Gorge in the Manawatu River system, near Woodville (Fig. 14.3, arrow 14) has never been authenticated or repeated, and the failure to find it again throws doubt on its authenticity. There is another, much more recent (2002), Manawatu record just west of the gorge (near Ashhurst), which is also distinctively distant from nearest other known populations (Fig. 14.3, arrow 14).

Brown mudfish is otherwise absent from all river systems draining eastwards from both the Ruahine Ranges to the north – Tukituki River and northern branches of the Manawatu Rivers and the Tararua Ranges to the south (southern branches of the Manawatu River: Fig. 14.3, arrow 15). It thus seems to have generally failed to invade the northern-central Wairarapa, and it is not known further to the north into southern Hawkes Bay.

In the South Island, brown mudfish is known on the West Coast from a wetland near Mangarakau in the north (a little south of the Whanganui Inlet near the north-western tip of the South Island – Fig. 14.3, arrow 6), and southwards from there. There are no records of brown mudfish to the east, from the freshwater wetlands of the land areas of Tasman or Golden Bays (Fig. 14.3, arrow 7), though relatively few wetlands remain in this intensively developed area. Given the quite wide range of this species in the southwestern North Island, discussed in the previous paragraph, the former presence of populations of brown mudfish in freshwater habitats across Golden and Tasman Bays seems not unlikely, but there are no confirmed records. Stokell (1955) in his popular book, recorded brown mudfish from “Nelson” (though he had not mentioned this in his 1949 taxonomic revision of the New Zealand Galaxiidae). Precisely what he meant by “Nelson” is unclear. He could have been referring to the Buller area of the West Coast, since this was regarded as part of the ‘Nelson Province’ in earlier colonial times. This is the only known explicit reference to brown mudfish in ‘Nelson’. The species’ West Coast range extends as far south as about Okarito (Fig. 14.2, arrow 8), and so it extends well into the area regarded as seriously impacted by the last advance of Pleistocene glaciation (Soons 1992), from which other non-diadromous species, such as dwarf galaxias (see Chapter 12) and upland bully (see Chapter 15) are not recorded.

Presence of brown mudfish on both sides of Cook Strait (Fig. 14.3, arrows 6, 13, and 14) creates no novel biogeographical scenarios, as the North and South Islands have been physically connected in the past – both during the Pleistocene glaciation, when there were significantly lowered sea levels (Fig. 14.4), and also much earlier in the Pliocene when, even though much of the southern North Island was submerged, there was a land connection across Cook Strait to an area of land in the

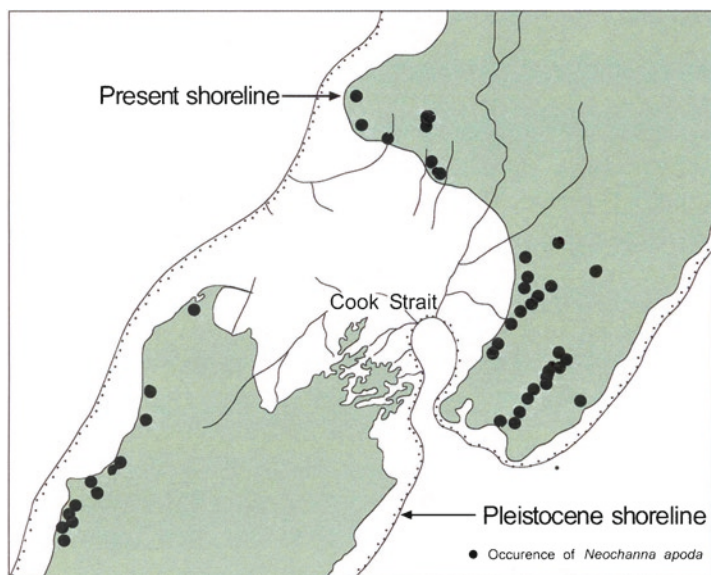


Fig. 14.4 Shoreline of central New Zealand in the Pleistocene, showing land connection across Cook Strait, where there was likely confluence of southern North Island and northern South Island river drainages (from Fleming, 1979), and the distribution of brown mudfish, *Neochanna apoda*

Whanganui area (known as the “Wanganui-Marlborough Shield” – Lewis and Carter 1994; Lewis et al. 1994) (see Fig. 3.3, arrow 2). There are thus at least two periods when there was a land connection across Cook Strait. Any Pleistocene land connection implicated in the presence of brown mudfish on both sides of Cook Strait was probably in the northern sector of the strait, as its southeastern sector is deep ocean, making a Pleistocene land connection across this sector seems unlikely (and it isn’t argued for by any of the geologists – Fleming 1979; Lewis and Carter 1994; Lewis et al. 1994; Newnham et al. 1999). Thus Pleistocene land connection was probably between the southwestern North Island and the northwestern South Island (see Figs. 3.4, 14.4), at which time Fleming (1979) showed various major southern North Island and northern South Island river systems to be confluent across the broad expanse of low-elevation emergent land that joined the North and South Islands.

14.5 Canterbury Mudfish, *Neochanna burrowsius*, in the Eastern South Island

The Canterbury mudfish *N. burrowsius* (Fig. 14.3 – red symbols), is found in the eastern South Island from a little north of Banks Peninsula (near the coast – Fig. 14.3, arrow 12, as well as a little further inland, though still only at relatively low elevations towards the upper edge of the Canterbury Plains and up to 400 m

altitude, and south across the Canterbury Plains to the Waitaki River valley (arrow 9). Most authors (Skrzynski 1968; Cadwallader 1975; Eldon 1979a; McDowall 1990; Davey et al. 2003) have reported Canterbury mudfish absent south of the Waitaki River but recent sampling has shown it to be present in a number of wetlands and springs along the southern fringes of the river channel itself. These findings may have little biogeographical significance, given the propensity for the large braided rivers of the eastern South Island, like the Waitaki, to shift channels and anastomose across the Canterbury Plains during floods. The absence of Canterbury mudfish more widely in the Waitaki River floodplain south of the river channel, but its presence only along the very fringes of the river might suggest that the species arrived in these southern sites relatively recently. Genetic examination of the southern populations would be interesting.

Genetic studies of Canterbury mudfish by Davey et al. (2003) revealed little divergence between populations and rather less molecular diversity within them than has been reported for other New Zealand mudfishes (Gleeson et al. 1998). They attributed this to “recent dispersal from a small [ancestral] historical population, and related periodic bottlenecks within individual populations.” Structuring of the little divergence among populations is significant, with only one haplotype being present at more than one site, prompting Gleeson et al. (1998) to argue for recent dispersal southwards across the Canterbury Plains – the genetics give the impression of a series of ‘founder’ populations with very narrow ancestries. These findings are not surprising, given the ephemeral habitats commonly occupied by Canterbury mudfish, with isolated habitats often reduced to small pockets where a few fish may survive dewatering and become the source for re-expansion when conditions later improve (O’Brien and Dunn 2005, 2007). It is quite possible that some of this low genetic diversity has quite recent origins, and results from fragmentation of populations and genetic bottlenecks caused by localised decline in abundance relating to anthropogenic habitat deterioration, particularly very intensive wetland drainage associated with pastoral farming (McDowall 1998) – though it has evidently not obscured the basal position of Canterbury mudfish among the five species of *Neochanna*. Deeper differences between populations north and south of the Rakaia River (Fig. 14.3, arrows 10 and 11) suggest historical separation; groupings of the populations derived from molecular data are consistent with known geographical distributions. Retention of pelvic fins in Canterbury mudfish, albeit small and with few rays (McDowall 1990), suggests a relatively basal position for this species among the mainland New Zealand mudfish species.

The separation of [Canterbury+Chathams mudfishes] from other mudfishes to the west and north by the Southern Alps (which have been rising only since some time in the Pliocene – Fleming 1979; McGlone 1985; Whitehouse and Pearce 1992; Campbell and Hutching 2007), may imply a vicariant speciation event resulting from the mountain uplift. Absence of any *Neochanna* mudfishes in Otago and Southland, might suggest that the Canterbury species has spread southwards across the Canterbury Plains, as these formed by erosion from the rising Southern Alps during Pliocene to recent times (absence from Otago and Southland is consistent with this conclusion).

14.6 *Neochanna rekohua*, a Mudfish on the Chatham Islands

The Chatham Island mudfish (Fig. 14.3 – green symbols, arrow 21), *Neochanna rekohua*, is known only from two small peat-land lakes in southern sector of Chatham Island, the principal island in the small group about 800 km east of the main islands of New Zealand. However, there are additional, similar, small lakes nearby that have not yet been investigated, and the Chatham mudfish may be a little more widespread than is presently known. Morphological data (well-developed pelvic fins with seven rays as in most *Galaxias* species) suggest that the Chatham Islands species is a sister clade to all other New Zealand species (McDowall 2004), whereas molecular data suggest that the Chatham and Canterbury mudfishes may share a closest common ancestry (Waters and McDowall 2005), this pair then being the sister clade of all other New Zealand species. Neither cladogram poses insuperable issues for understanding mudfish biogeography. The Chatham Islands mudfish, like the islands' entire terrestrial/freshwater biota, must have got there relatively recently if the island did, as Campbell and Hutching (2007) hypothesise, disappear entirely under the sea until it began to emerge perhaps only a few million years ago, though there was formerly clearly land present there much earlier, in the Cretaceous. Molecular studies are needed to date the divergence of Canterbury and Chatham mudfishes, and the dates will be of much interest, given the belief that the Chatham Islands are relatively recently emergent (Campbell et al. 1993, 2009; Campbell and Hutching 2007).

14.7 No *Neochanna* Mudfishes in Southern New Zealand

As noted above, there are no *Neochanna* mudfishes in Otago and Southland, and that fact is interesting given that this is one of the most ancient landforms in New Zealand (Craw and Norris 2003), and might suggest that the spread of mudfishes across the New Zealand landscape is relatively recent and that the group originated in northern New Zealand, though such an hypothesis might be inconsistent with the Canterbury mudfish being basal to the other more northern species.

The types of habitats that mudfish inhabit (they are often found in small wetland remnants that tend to dry up) mean that all mudfish populations are vulnerable to habitat loss and severe population bottlenecks, or local extirpation (and probably much more severely now than prior to human colonisation (as described by Eldon 1968, 1978, 1979a, b; Eldon et al. 1978; O'Brien 2007). This is likely to have had strong genetic effects, as observed by Davey et al. (2003) for Canterbury mudfish, and would include:

1. Selection for survival characteristics; as well as
2. A major loss of genetic diversity; but also perhaps
3. The development of local stocks in each isolated habitat fragment or area as the populations rebuilt

While it is certain that dewatering of wetlands became more prevalent following the European settlement of New Zealand, beginning in the mid-nineteenth century, the ability of mudfishes to aestivate during such events suggests that such stresses have long been a feature of mudfish ecological history.

References

- Brook FJ (1999) Stratigraphy and landsnail faunas of Late Holocene coastal dunes, Tokerau Beach, northern New Zealand. *J R Soc N Z* 29:337–359
- Cadwallader PL (1975) Distribution and ecology of the Canterbury mudfish, *Neochanna burrowsius* (Phillipps) (Salmoniformes: Galaxiidae). *J R Soc N Z* 5:21–30
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Campbell HJ, Andrews P, Beu AG (1993) Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. *N Z Inst Geol Nucl Sci Monog* 2:1–269
- Campbell HJ, Begg J, Beu A, Carter B, Curtis N, Davies G, Emberson R, Given D, Goldberg J, Holt K, Hoernli K, Malahoff A, Mildenhall D, Landis C, Paterson A, Trewick S (2009) Geological considerations relating to the Chatham Islands, mainland New Zealand and the history of New Zealand terrestrial life. *Geology and Genes IV. Geol Soc N Z Misc Publ* 126:5–6
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 17–34
- Davey ML, O'Brien L, Ling N, Gleeson DM (2003) Population genetic structure of the Canterbury mudfish (*Neochanna burrowsius*): biogeography and conservation implications. *N Z J Mar Freshwater Res* 37:14–22
- Eldon GA (1968) Notes on the presence of the brown mudfish (*Neochanna apoda* Günther) on the west coast of the South Island of New Zealand. *N Z J Mar Freshwater Res* 2:37–48
- Eldon GA (1978) The life history of *Neochanna apoda* Günther (Pisces: Galaxiidae). *N Z Min Agric Fish, Fish Res Bull* 19:1–44
- Eldon GA (1979a) Habitat and interspecific relationships of the Canterbury mudfish, *Neochanna burrowsius* (Salmoniformes: Galaxiidae). *N Z J Mar Freshwater Res* 13:111–119
- Eldon GA (1979b) Breeding, growth and aestivation of the Canterbury mudfish, *Neochanna burrowsius* (Salmoniformes: Galaxiidae). *N Z J Mar Freshwater Res* 13:331–346
- Eldon GA, Howden PJ, Howden DB (1978) Reduction of a population of Canterbury mudfish *Neochanna burrowsius* (Galaxiidae) by drought. *N Z J Mar Freshwater Res* 12:313–321
- Eyles RJ, McConchie JA (1992) Wellington. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 382–406
- Fleming CA (1979) *The geological history of New Zealand and its life*. Auckland University Press, Auckland, N Z, 141 pp
- Fulton W (1986) The Tasmanian mudfish, *Galaxias cleaveri*. *Fish Sahul* 4:150–151
- Gleeson DM, Howitt RLJ, Ling N (1998) Phylogeography of the black mudfish, *Neochanna diversus* (Galaxiidae). *Geol Soc N Z Misc Publ* 97:27–30
- Gleeson DM, Howitt RLJ, Ling N (1999) Genetic variation, population structure and cryptic species within the black mudfish, *Neochanna diversus*, an endemic galaxiid from New Zealand. *Mol Ecol* 8:47–57
- Kamp JJ (1992) Landforms of Wairarapa: a geological perspective. Wellington. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. N Z, Longman Paul, Auckland, pp 367–381
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) *Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea*

- conference, Christchurch, New Zealand, 27–30 November, 1992 Balkema. Rotterdam, The Netherlands, pp 119–137
- Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Mar Geol* 116:293–312
- Ling N, Gleeson DM (2001) A new species of mudfish, *Neochanna* (Teleostei: Galaxiidae) from northern New Zealand. *J R Soc N Z* 31:385–392
- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species; the ‘new’ biodiversity and evolutionary significant units among New Zealand’s galaxiid fishes. *J Fish Biol* 59(Suppl A):209–222
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1996) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1997) Affinities, generic classification, and biogeography of the Australian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Rec Aust Mus* 49:121–137
- McDowall RM (1998) Once were wetlands. *Fish Game N Z* 20:31–39
- McDowall RM (1999) Just hanging around for some fresh air thanks! Survival adaptations of the mudfish. *Water Atmos* 7(2):7–8
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McGlone MS (1985) Plant biogeography and the late Cenozoic history of New Zealand. *N Z J Bot* 23:723–749
- Meredith AS, Davie PS, Forster ME (1982) Oxygen uptake by the skin of the Canterbury mudfish, *Neochanna burrowsius*. *N Z J Zool* 9:387–390
- Neall V (1992) Landforms of Taranaki and the Wanganui lowlands. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 287–307
- Newnham RM, Lowe DJ, Williams PW (1999) Quaternary environmental change in New Zealand: a review. *Prog Phys Geog* 23:567–610
- O’Brien LK (2007) Size dependent strategies in response to diet by *Neochanna burrowsius*. *N Z Nat Sci* 32:21–28
- O’Brien LK, Dunn N (2005) Captive management of mudfish *Neochanna* (Teleostei: Galaxiidae) spp. *N Z Dep Cons Res Devel Ser* 205:1–29
- O’Brien LK, Dunn N (2007) Mudfish (*Neochanna*: Galaxiidae) literature review. *Sci Conserv* 277:1–89
- Skrzynski W (1968) The Canterbury mudfish, *Galaxias burrowsius* - a vanishing species. *N Z J Mar Freshwater Res* 2:688–697
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 439–455
- Stokell G (1949) The systematic arrangement of the New Zealand Galaxiidae. Part II. Species classification. *Trans R Soc N Z* 77:472–496
- Stokell G (1955) Freshwater fishes of New Zealand. Simpson & Williams, Christchurch, N Z, 145 pp
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, White RWG (1997) Molecular phylogeny and biogeography of the Tasmanian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Aust J Zool* 45:39–48
- Whitehouse IE, Pearce AJ (1992) Shaping the mountains of New Zealand. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 144–160

Chapter 15

Distribution and Biogeography of the Non-diadromous *Gobiomorphus* Bullies

Abstract There are three species of non-diadromous *Gobiomorphus* bullies. One of these is a landlocked derivative of the diadromous common bully, and is found in a few small, post-glacial tarns in Marlborough. The other two are widespread, one entirely in the North Island and the other in the southern North Island, South Island and Stewart Island. A broad area of overlap in the southern North Island probably involved invasion of this area from both north and south when this region emerged from marine submergence in the Pliocene. Absence from the northeastern North Island reflects Holocene to Recent volcanism there, and absence from central/southern Westland relates to the effects of glaciation.

Keywords Glaciation • *Gobiomorphus* • Pleistocene • Pliocene submersion • volcanism

15.1 Non-diadromous Species of *Gobiomorphus* Bully

There are three New Zealand non-diadromous species of *Gobiomorphus* that comprise:

Tarndale bully, *Gobiomorphus alpinus* (Fig. 15.1), which is present in several high elevation tarns in close proximity in sub-montane inland Marlborough (Figs. 15.2 and 15.3 – green symbol), and is regarded as a landlocked derivative of the common bully (McDowall 1994; Smith et al. 2003; McDowall and Stevens 2007; Stevens and Hicks 2009) and bears no close relationship with the other non-diadromous species; and

Cran's bully, *Gb. basalis*, and upland bully, *Gb. breviceps* (Fig. 15.2), which are widespread across New Zealand, Cran's bully only, and widely, in the North Island, and upland bully primarily in the South Island and Stewart Island, but penetrating north into the southern North Island, where Cran's bully and upland bully have widely overlapping distributions (Fig. 15.2). The relationships of these two species, to each other, or of either or both to other, diadromous New Zealand bully species, have been elucidated by the recent genetic and morphological studies of Stevens and Hicks (2009).

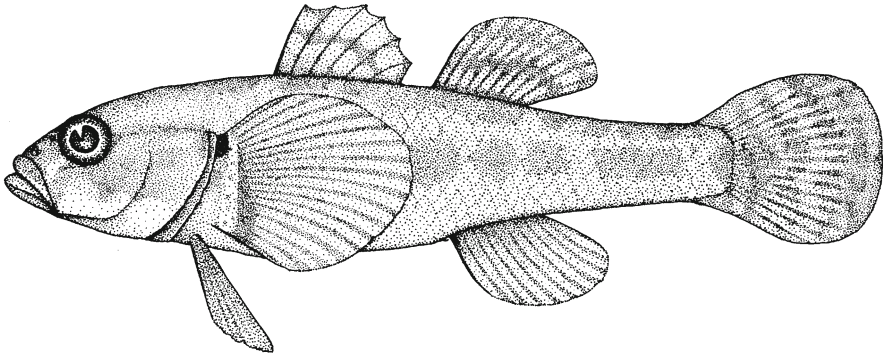


Fig. 15.1 Tarndale bully, *Gobiomorphus alpinus*, female, 74 mm T.L., one of the non-diadromous bully species

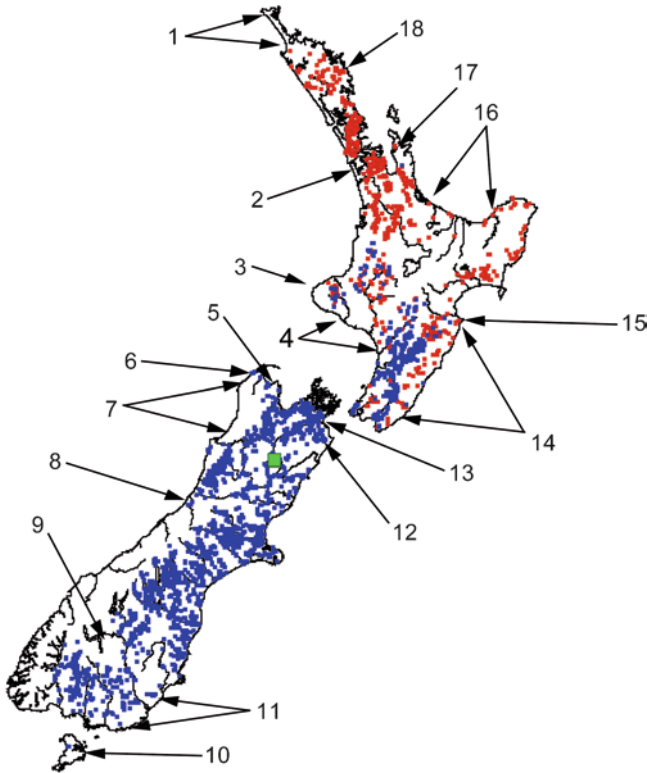


Fig. 15.2 Distributions of non-diadromous bullies: Cran's bully, *Gobiomorphus basalis*; (■); upland bully, *Gb. breviceps* (■); Tarndale bully, *Gb. alpinus* (■). **Arrows** – ↑1: absence from Aupouri Peninsula; ↑2: Mokau River; ↑3: absence to west of Mount Taranaki; ↑4: Intermittent presence along Wellington coastline catchments; ↑5: Golden Bay; ↑6: Whanganui Inlet; ↑7: Kahurangi National Park; ↑8: Hokitika River; ↑9: Shotover River, tributary of the Kawarau River, Clutha River system; ↑10: Stewart Island; ↑11: Southland Plains; ↑12: river systems of Marlborough; ↑13: Marlborough Sounds; ↑14: area of overlap across southern North Island; ↑15: rivers of southern Hawkes Bay; ↑16: area of absence across North Island east of Taupo Volcano eruption site; ↑17: sites on northern Coromandel Peninsula; ↑18: widespread north of Auckland Isthmus

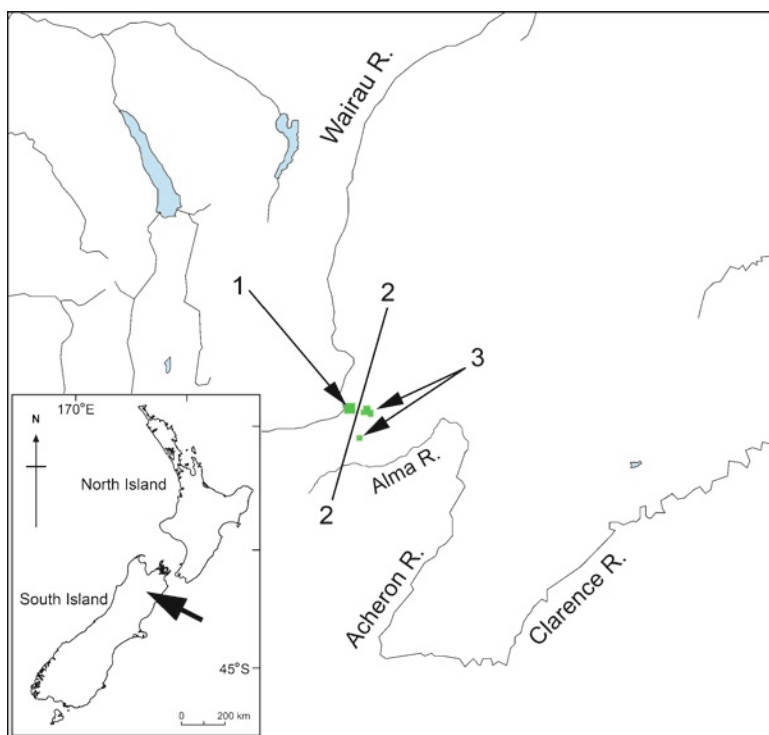


Fig. 15.3 Distribution of the Tarndale bully, *Gobiomorphus alpinus*, in upland Marlborough. **Arrows** – ↑1: Fish Lake, which drains into the upper reaches of the Wairau River system; line 2: indicates a low, narrow divide between the Wairau and Clarence Rivers; ↑3: Bowscale Tarn, Island Lake, and other small tarns that drain into the upper reaches of the Clarence River)

15.2 The Tarndale Bully, *Gobiomorphus alpinus*, in Inland Northern South Island

As just discussed, the Tarndale bully, *Gb. alpinus* seems to be a landlocked derivative of the diadromous common bully (McDowall 1994; Smith et al. 2003; McDowall and Stevens 2007; Stevens and Hicks 2009). However, Smith et al. (2003) examined the taxonomic status of the Tarndale bully based largely on molecular information, the geological history of this area and how this may have influenced the derivation and distributions of these populations, and they concluded, on several stated grounds, that this morph should be regarded as no more than an ecophenotype of the diadromous common bully. In my view they were incorrect in every reason suggested. They pointed to some distinctive morphological characters, particularly differences in fin ray counts and vertebrae, but

attributed these to the influence of the high elevations at which the species is found, despite there being no evidence in other bullies for environmental influences on such characters. And they pointed to the lack of haplotypes in the mitochondrial genome of Tarndale bully different from those of the diadromous common bully, though if this logic is pursued, then both these bully species are also no different from Cran's bully, which also exhibits no sequence differences in the mitochondrial genome, though they did not recommend that this species, too, should be synonymised, and this would be ludicrous, given the substantial morphological and behavioural differences between common and Cran's bullies (McDowall 1990).

I recognise the Tarndale bully populations as a distinct species (McDowall and Stevens 2007). It is found only in a series of small, alpine tarns in close proximity in the headwaters of the Clarence River (Bowscale Tarn, Island Lake, and nearby small, un-named tarns) and the Wairau River (Fish Lake) in inland Marlborough (Figs. 15.2 and 15.3 – green symbols).

As Smith et al. (2003) reported, the area of the former Tarndale Station in which this bully is found, was heavily glaciated in the late Pleistocene (McAlpin 1992). The tarns occur in depressions created along the Awatere Fault, an extension of the New Zealand Alpine Fault (Bowen 1964; McAlpin 1992). Ice advanced extensively in the Waimea glaciation, c. 25,000 years ago, to envelope the present positions of the tarns and that area is regarded as having remained ice covered until around 18,000 years ago. At that time the uppermost, headwater tributaries of what is now the Wairau River, flowed east to join the Severn River, a Clarence River headwater. An ice-dammed lake filled the upper Wairau River valley, submerging the area now occupied by Fish Lake. When the ice retreated, uplift along the Awatere Fault disconnected some of the tributaries of the upper Clarence River and diverted them to the west to become part of the headwaters of the Wairau River. This included Fish Lake which retained its connection with what, as a result, became the uppermost tributaries of the Wairau River. The other 'Tarndale' lakes established fluvial connections with tributaries of the east-flowing upper Clarence River (Fig. 15.3), via the Alma and Acheron Rivers.

These populations of Tarndale bully are well isolated geographically from any known populations of common bully, the nearest of which, by water, are probably in the lower reaches of the Wairau, c. 160 km away by river, and the Clarence c. 220 km away. The geological evidence reviewed by Smith et al. (2003), and discussed above, suggests that these tarns (and thus presumably their fish populations) are unlikely to be more than c. 18,000 years old. On the other hand, presence of this species in tarns associated with both the upper Wairau and upper Clarence Rivers, may suggest that there may have been populations of this species in the area from a time before the development of the existing patterns of dual headwater tributary connections to both the Wairau and Clarence River catchments, just discussed. So, the Tarndale bully has a biogeography intimately involved with the geological histories of the upper Wairau and Clarence Rivers.

15.3 Two Further Widespread Non-diadromous Bullies, *Gobiomorphus basalis* and *G. breviceps*

There are two additional non-diadromous species: Cran's bully and upland bully. Their phylogenetic relationships, both to each other and to the various diadromous bully species, have recently been resolved by Stevens and Hicks (2009). Reduced scale coverage on the head could be regarded as indicative of a close relationship between upland and Cran's bully but Stevens and Hicks' phylogeny, if correct, means that reduced scalation has developed twice, or more often (or there has been reversion and scalation has become broader again in redfin and giant bullies). Notably, reduced scalation on the back of the head is true also of the diadromous bluegill bully, a taxon that Stevens and Hicks (2009) have shown to be the sister lineage of all other New Zealand species of *Gobiomorphus*, which probably implies multiple loss of head scales. Similarly, the distinctive polygonal facial blotches, which upland bully shares with bluegill bully (see Fig. 1.6) would superficially be regarded as heuristic, but again this seems unlikely. Given that it is true of the most basal species, the bluegill bully, these polygonal blotches could be a plesiomorphic character that has survived in upland bully, but has been lost in redfin, giant, common, and Tarndale bullies, or constitutes either a reversion or convergence in the upland bully. Whichever is true, the facial blotches seem uninformative of relationships. On the basis of their analysis of mtDNA, Stevens and Hicks (2009) concluded that these two non-diadromous species are not sister clades. Rather than that, the upland bully proves to be a sister lineage to a clade consisting of redfin and giant bully (both of these amphidromous – McDowall 1990), whereas Cran's bully is a sister taxon to a clade comprising common bully and Tarndale bully. This indicates that there has twice been loss of amphidromy in each of the lineages leading to upland and Cran's bullies, with further repeated loss in lacustrine populations of the basically amphidromous common bully, leading to the Tarndale bully, as discussed earlier in this chapter. Here is an instance in which the most parsimonious lineage splitting events, involving loss of amphidromy just once, seems incorrect – but there are very numerous, almost certainly independently derived lacustrine populations of the normally diadromous common bully, so that we can be sure that loss of the marine migratory juvenile life stage has happened often. The apparent frequency with which amphidromy is lost in common bully is a likely harbinger of patterns of loss in the other lineages. It is consistent too with the apparent ease and frequency with which diadromy is lost in other New Zealand freshwater fish lineages, such as common smelt (Retropinnidae) and koaro (Galaxiidae – see Chapter 7).

Several lower-level taxonomic issues remain unresolved for both upland and Cran's bullies. Evidence from differences in egg size and lack of interfertility between northern and southern populations of Cran's bully strongly hints at the present taxonomy failing to recognise that, what is alluded to as *Gb. basalis*, is actually two species (author of book, unpublished), though the molecular (mtDNA) study of Stevens and Hicks (2009) did not indicate such a separation of stocks. Molecular data do, however, suggest deep genetic structuring of populations of upland bully in the northern South Island (Smith et al. 2003, 2005 – Fig. 15.4;

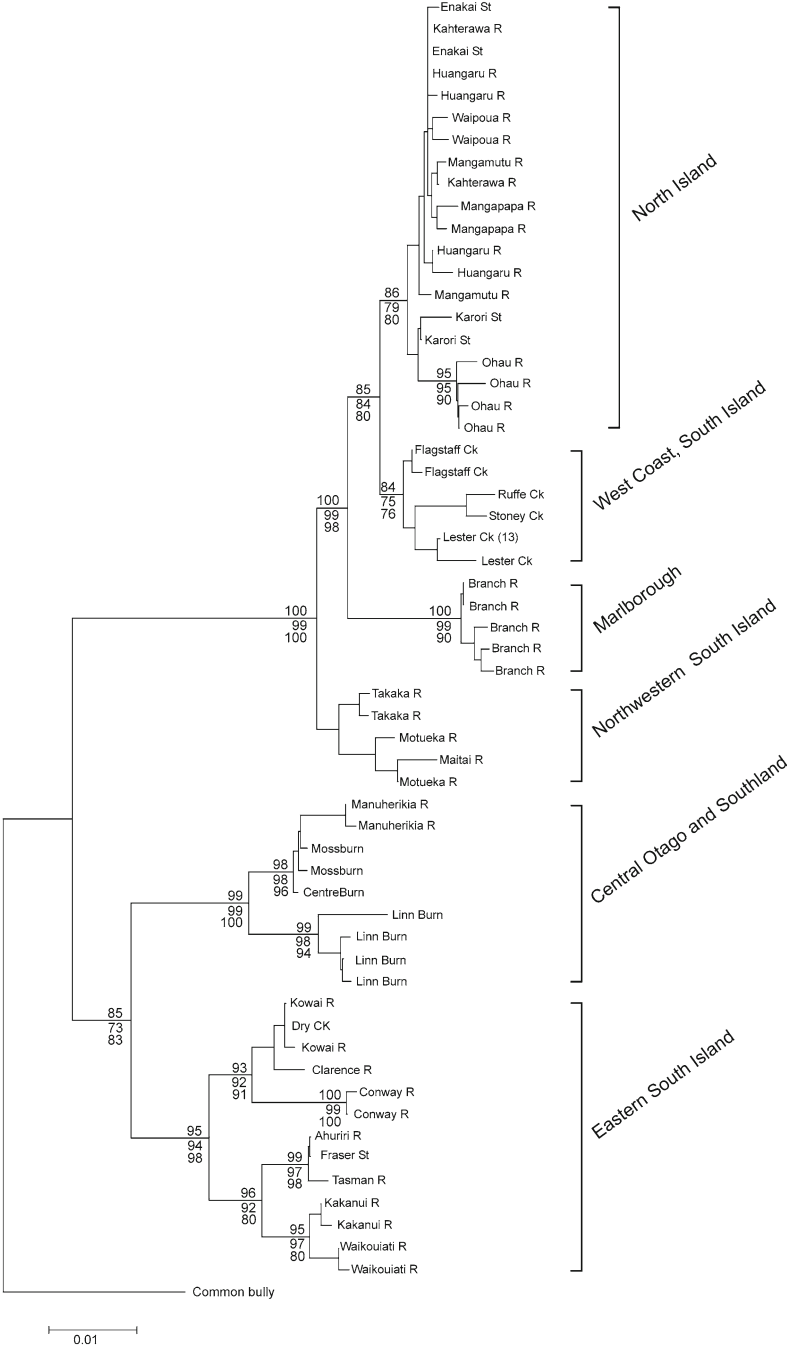


Fig. 15.4 Molecular evidence for stock relationships of populations of upland bully, *Gobiomorphus breviceps* (adapted from Smith et al., 2005)

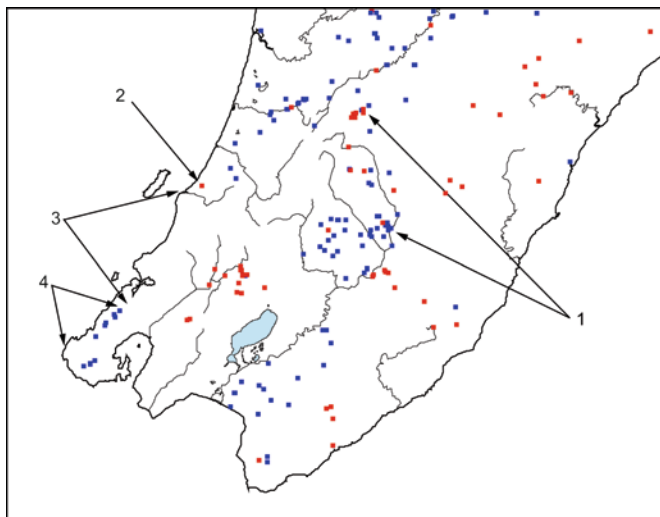


Fig. 15.5 Broadly overlapping distribution of Cran's bully, *Gobiomorphus basalis* (●) and upland bully, *Gb. breviceps* (●) in the southern North Island. **Arrows** – ↑1: confirmed instance of co-occurrence of Cran's bully and upland bully; ↑2: Waikanae River; ↑3: absence along Wellington coastline; ↑4: isolates of upland bully on the Wellington Peninsula

Stevens and Hicks 2009) and, again, we may be dealing here with more than one species. Until these questions have been dealt with, the group's broad-scale biogeography cannot be further resolved with any finality.

Cran's (Fig. 15.2 – red symbols) and upland bullies (Fig. 15.2 – blue symbols) appear to have centres of distribution on the North and South Islands, respectively, with a broad zone of range overlap in the southern North Island (Fig. 15.2, arrow 14, Fig. 15.5). This zone of overlap is roughly coincident with the area of the North Island that was submerged by sea during the Pliocene (see Fig. 3.3) – perhaps giving the appearance of both species having invaded the area, generating the geographical overlap, since it became emergent during the Pliocene (Lewis and Carter 1994) – presumably involving invasion by Cran's bully from the north and by upland bully from the south, across Cook Strait at a time of a land connection. Further molecular studies are needed to clarify this question. There are quite serious identification problems with these two non-diadromous bullies, and although they clearly have broadly overlapping distributions in the southern North Island, records of both species from the same streams may cast doubt on some of the identifications; however, both morphological and molecular data show that both species show certain site sympatry at least one site in the Wairarapa (M.K. Joy, 2007, personal communication; author of book, unpublished).

Setting aside the unresolved question of unrecognised taxonomic diversity in these populations: the northern limits of Cran's bully in the far northern North Island are to the south of the Aupouri Peninsula (Fig. 15.2, arrow 1), and the

species' range extends southwards through the Auckland Isthmus, and as far as the Wellington area of the southern North Island (Fig. 15.2 and 15.5 – red symbols). Cran's bully's apparent failure to occupy the Aupouri Peninsula in the far north of the North Island (Fig. 15.2, arrow 1), may imply that it was slow to move north after formation of the tombolo joining the body of Northland to the far north (Brook 1999). Alternatively, however, it may simply, in part or in entirety, be that there are very limited, suitable, fluvial, rocky-stream habitats north of around Kaitaia – or perhaps there has been a combination of both influences.

Cran's bully is widely absent across a broad swath of landscape in the central North Island, particularly around Lake Taupo and to the east and northeast of the Taupo volcanic zone towards East Cape (Fig. 15.2, arrow 16). Absence may well be due to prolonged volcanism events in this area – especially, perhaps, the most recent, major Taupo eruption AD c.186 (Wilson 1993; Wilson and Houghton 1993; McDowall 1996), though it is possible that there remain some residual impacts that date back to earlier volcanism lasting for as long as 50,000 years (McGlone 1985; Lowe and Green 1992; Wilson 1993; Wilson and Houghton 1993; Newnham et al. 1999; Campbell and Hutching 2007). Cran's bully is so rarely reported in the central North Island – north from Lake Taupo into the upper reaches of the Waikato River as far as Lake Karapiro, and also in the rivers systems of the western Bay of Plenty (Kaituna River in the west, and east as far as the Waioeka River) – that some confirmation of identifications of occasional records from within the area of greatest ash deposition is needed. However, sporadic presence of non-diadromous bully species in rivers draining across the low elevation Bay of Plenty district has a precedent in similarly sporadic presence in this area of dwarf galaxias (see Fig. 12.2 – blue symbols arrow 21). These could be pockets of survival there of the effects of past volcanism. Presence of Cran's bully in the central North Island 'resumes' west and south of the zone of greatest ash deposition, and it is present widely in the western inland branches of the Whanganui River and the upper Whangaehu River. Absence from eastern headwater tributaries of the Whangaehu River may reflect the impacts of periodic break-out of lahars from the crater lake of volcanic Mount Ruapehu (Williams and Keys 2008).

Cran's bully is also absent from all but the inland (eastern) drainages of the Mount Taranaki Ring Plain (Fig. 15.2 – red symbols, arrow 3; and Fig. 15.6 – red symbols), and this absence may reflect the impacts of recent volcanic activity there (most recently only 300 years ago – Neall 1992). This species is present in some of the southern Hawkes Bay rivers (Tukituki, Ngaruroro – Fig. 15.2, arrow 15; and see Fig. 17.5b, arrow 1), but it is so rare in both the northern and southern arms of the Manawatu River in the Wairarapa east of the Manawatu Gorge, that the identifications may be in doubt for some of these records, as well. Most Wairarapa records are from east-flowing coastal drainages, plus a few in the upper Ruamahanga to the south. There are also confirmed pockets of Cran's bully in the upper reaches of the Hutt River, near Wellington (Fig. 15.5, arrow 5 – red symbols), so the species has somewhat sporadic southern presence.

Upland bully is present widely but only intermittently in the southern North Island, where it exhibits a broad area of overlap with Cran's bully (Fig. 15.2,

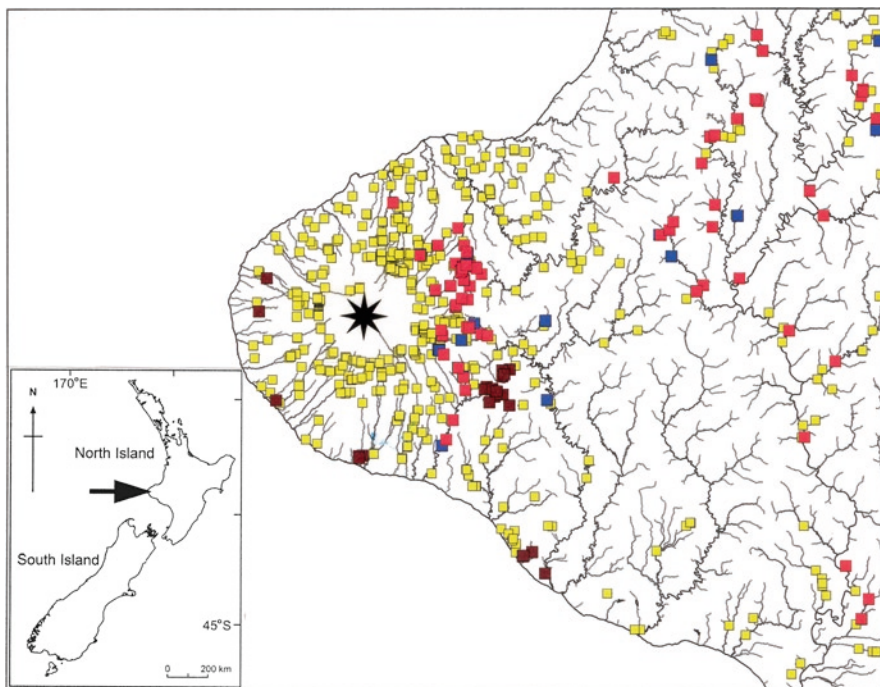


Fig. 15.6 Distributions of Cran's bully, *Gobiomorphus basalis* (■), upland bully, *Gb. breviceps* (■), brown mudfish, *Neochanna apoda* (■), and koura or freshwater crayfish, *Paranephrops planifrons* (■) on the ring-plain around Mount Taranaki (★Mount Taranaki)

arrow 14; Fig. 15.5 – blue symbols), mentioned above, though site sympatry of the two species is unusual (and, as also noted above, some apparent instances of co-occurrence of Cran's and upland bullies (Fig. 15.5, arrow 1) may indicate a need to check identifications). The North Island range of upland bully seems to be primarily in river systems that drain into Cook Strait/South Taranaki Bight – and thus perhaps in rivers that may once have been confluent with rivers from the northern South Island during lowered Pleistocene sea levels when there was a land connection across Cook Strait (Fleming 1979; Lewis and Carter 1994; Lewis et al. 1994; Campbell and Hutching 2007).

There are a few records of upland bully from the Ngaruroro and Tukituki Rivers in southern Hawkes Bay (Fig. 15.2, arrow 15, and see Fig. 17.5a, arrow 1), and these, too, raise questions of identification (as above). However, some dispersion of this species north of the northern arm of the Manawatu River (in which this species is widespread and abundant), should not be discounted.

Smith et al. (2005) published molecular data, which show that populations of upland bully on the West Coast of the South Island are genetically closest to those from the North Island, and that these are closest to populations in Nelson

(Golden and Tasman Bays), while all of the above populations in the northern South Island and southern North Island, form a sister group to those from the rest of the South Island, east and south of the Southern Alps (Fig. 15.4). These sets of relationships are consistent with invasion of the southern North Island from northern South Island populations at a time of land connections across the strait, as suggested above. Like Cran's bully, upland bully is absent from drainages to the west of Mount Taranaki though it, too, is widely present in river systems to the east of the mountain (Fig. 15.2, arrow 3; Fig. 15.6 – blue symbols).

There are some intriguing areas of presence/absence of upland bully in the Wellington area. This species turns up 'here and there' for no presently understood reason, e.g. in several small streams on the Wellington Peninsula, west of the city (South Karori Stream, Ohariu Stream – Fig. 15.5, arrow 4 – blue symbols), though it is absent from the mainstem Makara Stream into which the Ohariu Stream flows. It is absent from other rivers along the western Wellington coastline as from tributaries of the southern arm of Porirua Harbour in the south as far north as the Waikanae River catchment in the north (Fig. 15.5, arrow 3), but it is recorded from several catchment to the north of the Waikanae River (Fig. 15.5, arrow 2).

Upland bully is very widespread across the South Island, and is present also on Stewart Island (Fig. 15.2, arrow 10), but is rarely found in west-flowing drainages along the west coast of the South Island north of the lower Buller River (Kahurangi National Park – Jowett et al. 1998) (Fig. 15.2, arrow 7), though it is present in streams draining into the Whanganui Inlet, with records also from the Patarau River south of the inlet, and at Mangarakau (Fig. 15.2, arrow 6). Further to the east it is absent from the rivers Golden Bay, though present in the Takaka River in the east of Golden Bay (Fig. 15.2, arrow 5) and is widespread in the catchments of Tasman Bay, further to the east again. On the West Coast, the species is found as far south as the Hokitika River (Fig. 15.2, arrow 8), but no further, another likely reflection of the impacts of Pleistocene glaciation in the western South Island (the 'beech gap' again). Though widely present inland from the Marlborough Sounds (Fig. 15.2, arrow 12) in the northeastern South Island, upland bully is absent from streams of the Marlborough Sounds, themselves (Fig. 15.2, arrow 13), and this absence seems likely to reflect historical rather than (ecological) habitat-suitability mechanisms.

Upland bully's very wide distribution across the South Island, from north to south and also on Stewart Island (Fig. 15.2, arrow 10) is distinctive by comparison with all other non-diadromous species, which are always much more regional/localised in occurrence. Its presence widely through the northern regions, with populations to the north and west as well as east and south of the Southern Alps, superficially indicates no evident effect of mountain building involving the Southern Alps on the distribution of this species. However, molecular data demonstrate a deep separation between populations from North Island/West Coast South Island, and those of the eastern and southern South Island (Smith et al. 2005) (Fig. 15.4), and this might be consistent with a vicariant event driven by uplift of the Southern Alps during the Pliocene and Pleistocene. These results show a need for further molecular and taxonomic study.

Smith et al.'s (2005) results show that lineages incorporating all of the North Island populations that they studied are derived in relationship to those from the northern South Island (Fig. 15.4), which is consistent with the North Island populations being derived from the south, perhaps post-dating the re-emergence of the southern North Island from its Pliocene submergence, and/or perhaps at a time when Cook Strait was bridged, as during the Pleistocene. Northwestern South Island lineages (Takaka and Motueka Rivers) are sister to those from Marlborough and West Coast (Fig. 15.4). Populations across the remainder of the eastern South Island (Canterbury to Southland) group together, but exhibit quite deep separation of populations from Otago and Southland, from those in Canterbury to North Otago. Thus, upland bully, though widespread in the eastern and southern South Island, also has molecular lineages there that exhibit some distinctive features, though this distribution also has some parallels with other taxa. Again, more study is needed, and results from fish originating around the Lewis Pass in the northern South Island will be interesting. There is a need to examine populations across the broad range of upland bully, particularly relative to the distribution of non-diadromous galaxiids, of the *Gl. vulgaris* complex, given the results of genetic studies of the *Gl. vulgaris* complex in the Maruia/Lewis Pass region (see Section 11.2.1), and the presence there of distinct lineages of the 'pencil-galaxias' complex (Fig. 12.2, arrow 1). And, as with the *Gl. vulgaris* species complex, patterns in this area need to be explored cognisant of the effects of Pleistocene glaciation in the Southern Alps. Absence of upland bully from the Nevis River, which formerly flowed south but now flows north to join the Kawarau River in the Clutha catchment (see Section 11.2.9) could be a result of upland bully arriving in Southland after the Nevis's flow was reversed. Certainly, upland bully has spread much more widely across Southland in a way that the non-migratory galaxiids in that area have not. Alternatively, upland bully could have been extirpated from the redirected Nevis during episodes of major climatic cooling in the Pleistocene.

Apart from one old (dubious) record from the Shotover River (Fig. 15.2, arrow 9; Fig. 15.7, arrow 5) – which has been removed from the NZFFD because it is so dubious (old and never repeated despite many other sampling locations in the vicinity) upland bully is unknown from the entire Lake Wakatipu/Kawarau River sub-catchment of the Clutha River (Fig. 15.7, arrow 5), including absence also from the Nevis River – despite that river's former southern Maitai connection, and where upland bully is widespread (see discussion of the idiosyncratic presence of Gollum galaxias in the Nevis, Section 11.2.8). It is largely lacking, too, from the Cardrona River, but it was found recently in one site there (Fig. 15.7, arrow 3) despite repeated earlier sampling at c. 50 sites, even though it is present in the mainstem Clutha near where the Cardrona River joins the Clutha (recall that the Cardrona once flowed south to join the Kawarau – Craw and Norris 2003); and upland bully is widespread in the Lindis (Fig. 15.7, arrow 1) and Manuherikia (arrow 2) Rivers. So, just in the Clutha catchment itself, there are what seem to be distinctive "absences" of upland bully. Similar questions apply in the Taieri River – where upland bully is very sparse (Fig. 15.7,

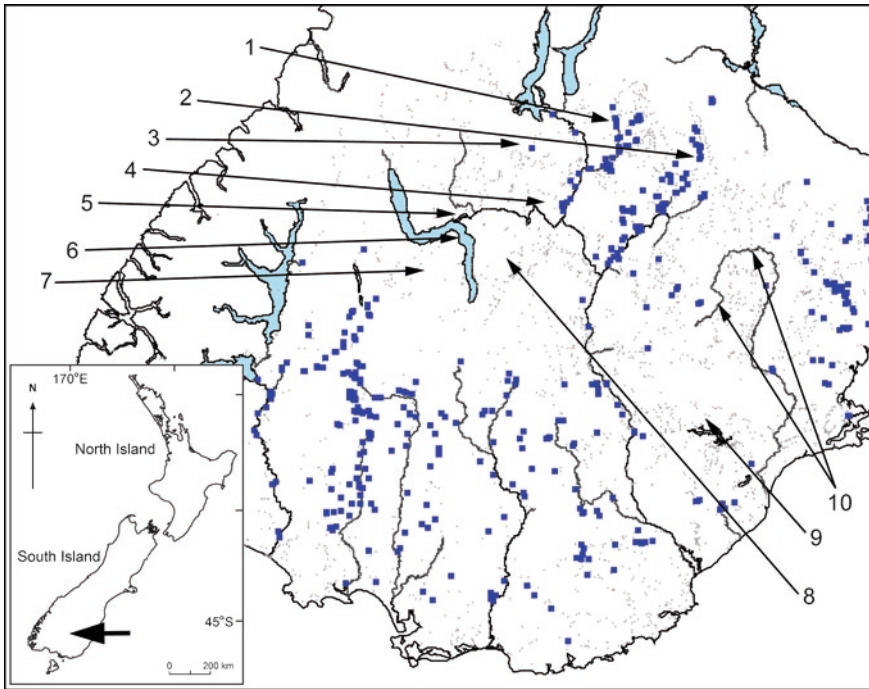


Fig. 15.7 Distribution of upland bully, *Gobiomorphus breviceps*, in the Clutha catchment Basin of Central Otago (■ (□ - all sampling sites). **Arrows** – ↑1: Lindis River; ↑2: Manuherikia River; ↑3: Cardrona River; ↑4: upper Clutha River mainstem; ↑5: Kawarau and Shotover Rivers; ↑6: Lochy River; ↑7: Von River; ↑8: Nevis River; ↑9: inland Waipori River site; ↑10: upper Taieri River

arrow 10), including total absence from the Waipori River (arrow 9), despite numerous sampling sites (see Allibone 1999). Recall that, despite the sparseness of upland bully in this area, it is an area of greater freshwater fish diversity than almost anywhere else in New Zealand. Richard Allibone (2007, personal communication) has observed recent instances of apparent disappearance of populations of upland bully in parts of the upper, sub-montane Taieri catchment. (Perhaps upland bully is living close to its thermal limits in the upper Taieri River catchment, and it may be vulnerable to local extirpation during severe winters). Existence of upland bullies in the cold high elevation Maniototo Plains (central Otago) could represent the most thermally extreme and challenging habitat occupied by any gobioid fish, globally.

Though further studies on these lineages are needed, there is enough to suggest that we may be looking at more than one species in what we now call *Gb. breviceps*, especially involving the deep divergences between (1) populations from the North Island, northern South Island north and west of the Southern Alps, and (2) those from the Kaikoura Ranges and further east and south of the Southern Alps.

References

- Allibone RM (1999) Impoundment and introductions: their impacts on native fish of the upper Waipori River, New Zealand. *J R Soc N Z* 29:291–299
- Bowen FE (1964) Sheet 15 – Buller. Geological map of New Zealand 1:250,000. Department of Scientific and Industrial Research, Wellington, N Z
- Brook FJ (1999) Stratigraphy and landsnail faunas of Late Holocene coastal dunes, Tokerau Beach, northern New Zealand. *J R Soc N Z* 29:337–359
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) The natural history of southern New Zealand. University of Otago Press, Dunedin, N Z, pp 17–34
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp
- Jowett IG, Hayes JW, Deans N, Eldon GA (1998) Comparisons of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. *N Z J Mar Freshwater Res* 32:307–322
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea conference, Christchurch, New Zealand, 27–30 November, 1992. Balkema, Rotterdam, The Netherlands, pp 119–137
- Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Mar Geol* 116:293–312
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 107–143
- McAlpin J (1992) Glacial geology of the upper Wairau Valley, Marlborough, New Zealand. *N Z J Geol Geophys* 35:211–222
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Reed, Auckland, N Z, 551 pp
- McDowall RM (1994) The Tarndale bully, *Gobiomorphus alpinus* (Pisces: Eleotridae) revisited and redescribed. *J R Soc N Z* 24:117–124
- McDowall RM (1996) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM, Stevens MA (2007) Taxonomic status of the Tarndale bully *Gobiomorphus alpinus* (Teleostei: Eleotridae), revisited – again. *J R Soc N Z* 37:15–29
- McGlone MS (1985) Plant biogeography and the late Cenozoic history of New Zealand. *N Z J Bot* 23:723–749
- Neall V (1992) Landforms of Taranaki and the Wanganui lowlands. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 287–307
- Newnham RM, Lowe DJ, Williams PW (1999) Quaternary environmental change in New Zealand: a review. *Prog Phys Geog* 23:567–610
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tarndale bully revisited with molecular markers: an ecophenotype of the common bully *Gobiomorphus cotidianus* (Pisces: Gobiidae). *J R Soc N Z* 33:663–673
- Smith PJ, McVeagh SM, Allibone R (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Williams K, Keys H (2008) Ruapehu erupts. Godwit, Auckland, N Z, 63 pp
- Wilson CJN (1993) Stratigraphy, chronology, styles and dynamics of late quaternary eruptions from Taupo volcano, New Zealand. *Phil Trans R Soc Lond A* 343:205–306
- Wilson CJN, Houghton BF (1993) The Taupo eruption. Institute of geological and nuclear sciences, Taupo, N Z, 6 pp

Chapter 16

A Biogeographical Synthesis:

1. The Big Picture

Abstract The freshwater fish fauna reflects a series of events in New Zealand's geological history, beginning with its origins in Gondwana, transoceanic dispersal, mostly from Australia, and derivations from fish species in the seas surrounding New Zealand; a probably perciform Miocene fossil represents a taxon not otherwise known from the country.

Keywords Derivations • Fossils • Gondwana • Marine derivations • Perciforms • Transoceanic dispersal

In this chapter I to draw together the diverse streams of data on distribution patterns across the whole New Zealand freshwater fish fauna. I seek to identify patterns that are common to more than one of the taxonomic groups discussed in previous chapters, or which suggest striking contrasts, and to view these patterns against what is known of New Zealand's geological and climatic history and the fauna's ecology, as also emphasised in earlier chapters: the observed distributions are, predictably, an amalgam of historical and ecological influences and processes (Endler 1982). Some of the subsections, in ensuing sections, relate to historical origins and dispersals, some to geography and geology, and others to evolutionary ecology and to the fish species' life histories. There is some inevitable repetition, here and there, as I try to generate a synthesis across taxonomic diversity and landscape history.

16.1 An Ancient Global Ancestry

It is becoming increasingly clear that, among the various families represented in New Zealand's freshwater fish fauna, the southern pouched lamprey has a very ancient heritage that is shared with the northern temperate petromyzontid lampreys (Gill et al. 2003). Similarly, the galaxiid and retropinnid fishes have ancient global ancestries, being among the most basal of the lower euteleost, soft-rayed fishes (McDowall 1969; Fink 1984; Johnson and Patterson 1996; Williams 1997), and again there are probably very ancient affinities of these southern families with northern

temperate families such as the Osmeridae and perhaps, to a lesser extent, the Salmonidae. Thus, at the broadest geographical scale, the Northern and Southern Hemisphere lampreys, along with the osmerid fishes in the north and the retropinnid/galaxiid fishes in the south, comprise some of the quite numerous known bi-temperate or anti-tropical distribution patterns (du Reitz 1940; Hubbs 1952; Schuster 1969; Oppen et al. 1993; BurrIDGE 2002). What might be regarded as distinctive is their presence in cool latitudes of both hemispheres at the family scale. How these north/south connections were established, historically, is unknown, but clearly there must have been some trans-tropical movement, perhaps at a time of cooler global climates and/or the taxa involved may formerly have had tolerances of higher temperatures than they seem to have, now. Whether these distributions are a consequence of oceanic dispersal, or involved hemispheric shifts on drifting continents, is unknown, and will probably always remain no more than the subject of speculation as to how the patterns developed. They may reflect very ancient geological and biological histories, and they have, perhaps, tempted the easy conclusion that equally-ancient development of the broad southern temperate distributions of the southern pouched lamprey and the galaxiid fishes is called for, i.e., that the broad Southern Hemisphere distributions of these fish groups also has vicariant, Gondwanan origins (Rosen 1974; Croizat et al. 1974; Craw 1979, 1989; Campos 1984; Brown and Lomolino 1998). But it does not necessarily follow, nor is it likely to prove so simple.

16.2 Widespread Taxa and Dispersal Ability

I argue here, as I have elsewhere and for decades (McDowall 1964, 1978, 1980, 1990, 2002, 2008; McDowall and Whitaker 1975), that an ancient genesis for the near circum-cold temperate distribution patterns of southern pouched lamprey and inanga is neither needed nor likely, but that the marine-living life stages of diadromous species, which are very widely present across all freshwater fish families present in New Zealand, provide an ability for long-distance, trans-oceanic dispersal. The timing of spread around the Southern Hemisphere is undetermined, though might be accessible through estimations using the molecular clock – though precise dating will probably always be elusive. Gill et al. (2003) have, suggested that there has been recent gene flow between Australian and Patagonian populations of the southern pouched lamprey, and given this result, New Zealand is likely to also be involved in similar patterns of dispersal. The same can be said of galaxiids (see below).

16.3 Is There a Gondwanan Heritage in the New Zealand Freshwater Fish Fauna?

When Zealandia became detached from Gondwana and began to drift northwards into the southwestern Pacific Ocean some time in the late Cretaceous, and so probably more than 80 million years ago (Cooper and Millener 1993; McLoughlin 2001;

Gibbs 2006; Campbell and Hutching 2007), it would undoubtedly have carried with it a distinctly Gondwanan biota of a wide range of plants and animals, including freshwater fishes, but which probably lacked a distinctive ‘New Zealand appearance’, especially by comparison with the modern taxa. Mildenhall (1980) and McGlone et al. (2001) identified a taxonomic shift in the New Zealand flora from:

- (i) A more cosmopolitan Gondwana flora shared with Australia, South America, Antarctic, South Africa, to some extent also India, and perhaps parts of South-east Asia to
- (ii) One of increasingly distinctive New Zealand character and endemism

Freshwater fishes were, no doubt, also involved in that process, though there is no clear, explicit evidence that any of the now-existing fauna has been derived directly and locally from that Gondwana heritage – not even the *Neochanna* mud-fishes, whose distributions Flannery (1984) thought must be that ancient – though it seems that they are probably not. The Australian-New Zealand connection evident in *Neochanna* seems substantially more recent than the late Cretaceous connection of New Zealand to Gondwana, given the presence of amphidromy in the Tasmanian species (Fulton 1986; Waters and White 1997; Waters and McDowall 2005: see Chapter 14). There are, however, some southern-temperate galaxiid affinities that might be more ancient, perhaps involving the Australian *Galaxiella* and the Chilean *Brachygalaxias* (Waters et al. 2002; McDowall and Waters 2004), and other groups, but diverse causations for phylogenetic relationships seem likely (and New Zealand was not implicated in this group, as far as we know). Further study is needed.

Thus, although some commentators have argued for the ancestry and origins of the New Zealand freshwater fish fauna to be ancient and to lie in these old Gondwanan faunas and land connections (Rosen 1974; Croizat et al. 1974; Craw 1979; Campos 1984), and though there can be little doubt that Zealandia would originally have had freshwater fishes of Gondwanan origins, the broad-scale derivations of the extant New Zealand freshwater fish fauna are probably related, substantially, to much more recent dispersal events (McDowall 1964, 1970, 1990, 2002; Waters and Burridge 1999; Waters et al. 2000). The question of dispersal remained rather intractable for decades because of the difficulties in verification/falsification of dispersal hypotheses, that for some observers became a matter for ridicule (see Chapter 8). The idea was assigned, by some, to a world of “make believe and pretense” (Croizat et al. 1974), “imagination” (Rosen 1974), or was described as “miraculous” (Craw 1979; Michaux 2000), which is interesting language from those ostensibly interested in rigorous biogeographical hypotheses. In part, the problems have been due to the difficulties in establishing testable dispersal hypotheses (Ball 1975), but this, to a substantial extent, has been an inevitable outcome of historical analyses.

Rosen (1974) argued vehemently for the galaxiid fishes as a whole having been essentially where they are “for a very long time”, and in a very restricted sense, at the family level, he may well have been right – as hinted at in Waters et al. (2002). But the explanations of existing patterns need not be seen as ‘all or nothing’ hypotheses – there is scope for causal diversity – common patterns need not have

common causes across wide time scales (McDowall 1978; Kodandaramaiah 2009). Rosen (1974) concluded that a “Gondwanaland hypothesis...simply accounts for the now disparate galaxiid population centers”. However, that is not necessarily so simple, nor do evolutionary history or biotic dispersal necessarily follow parsimonious pathways. The assumption that there was a uniform Gondwanan origin of all these taxa is only superficially simple, anyway, as amongst other complications is the need for morphological stasis in the very widely separated and ostensibly long separated populations of such widespread species as the southern pouched lamprey or the inanga. Moreover, the application of molecular sequencing techniques as a means of elucidating relationships (Avice 2000), and of assigning estimated dates to recency/antiquity of gene flow between disjunct taxa or populations, has a role to play in developing our understanding of biotic history especially providing a template for the distribution patterns, despite Ebach et al.’s (2003) cavalier dismissal of phylogeography as “insular and blinkered” (see Riddle 2009; Avice 2009). Molecular studies of the galaxiid fishes are consistently pointing to Cenozoic or more recent gene flow, at least across the Tasman Sea between Australia and New Zealand, and this is far too recently to implicate Gondwana in establishing these biotic connections, e.g., Waters and White (1997) dated the arrival of *Neochanna* mudfishes in New Zealand as probably as recently as Pliocene.

Thus the prospect cannot be discounted that some of the trans-Tasman, transoceanic gene flow (dispersal) by galaxiid has been relatively recent in the context of New Zealand’s geological history but that it has involved some elements in the fauna that may, at the same time, have had Gondwana connections/derivations in New Zealand, as possibly with the pencil galaxias complex. This conclusion does not rest entirely, however, with molecular data; other, and quite disparate, aspects of distributions and relationships are also consistent with the same dispersal explanation for New Zealand’s freshwater fishes: the relationship between distribution patterns and life history patterns, as already well discussed here is consistent with a dispersal biogeography, as is the recent arrival in New Zealand of the Australian spotted longfin eel; also, the parasite faunas of these fishes around southern lands give no hint of support for a vicariance biogeography (McDowall 2000, 2002). We seem to be looking, here, at sometimes relatively recent biogeographical/dispersal processes operating on a potentially ancient fish fauna that may once have been widespread, and on what are now the fragments of an equally ancient landmass. These are not necessarily ‘either-or’ scenarios, but quite possibly ‘some of both.’ This does not, perhaps, result in the relatively simple, uniform, consistent explanation that the panbiogeographers and cladistic biogeographers seek (Rosen 1974; Craw et al. 1998; Humphries and Parenti 1999; McCarthy et al. 2007); but then: ‘Why should it be simple?’ And of course those who are arguing for complete Oligocene submergence of New Zealand are faced with a need for the entire biota to be a dispersal one, animals, plants, the lot.

In nearly all instances New Zealand freshwater fishes are either diadromous (and those that are, are often seen as having a dispersal origin in New Zealand – McDowall 2002), or are derived from these diadromous species, either in New Zealand as in the *Galaxias vulgaris* species complex (McDowall 1970; Waters and Wallis 2001) or in

Australia, as in the *Neochanna* mudfishes (McDowall 1997, 2004) and, as well, probably, *Gobiomorphus* bullies (Stevens and Hicks 2009; Miles et al. 2009). This may not, however, be true of the ‘pencil-galaxias’ complex, which comprise a New Zealand ‘endemic’ of uncertain affinities, although they may prove to just be another local radiation of New Zealand origins.

16.4 Diverse External Origins

Though the relationships of New Zealand’s freshwater fishes seem largely to connect to the west and north-west, in southeastern Australia and Tasmania, there also clear indications of broader affinities that do not implicate Australia. Although some Australia-New Zealand freshwater fish distribution patterns are part of broad southern cool-temperate ranges (also involving Patagonian South America, and sometimes the Falkland Islands and South Africa – especially the galaxiids, but also the New Zealand pouched lamprey), other Australia/New Zealand patterns are part of broader taxonomic ranges extending into the warm-temperate Indo-Pacific and have little or no connection to the southern cool temperate at all (anguillid eels, for instance and eleotrid bullies). This is, in itself, interesting, as the variation in affinities suggests that there is no simple, unified, pattern of derivation/ancestry like that espoused by the panbiogeographers, despite some relationships having the appearance of being parallel. Do the panbiogeographers and vicariance biogeographers insist that *Gobiomorphus* has ancient Gondwanan connections too?

16.5 Species Are Derived from Local Seas

Torrentfish and black flounder are diadromous species whose ancestries appear to be in local seas, and there is little hint of broader-scale geographic origins or affinities of these freshwater taxa, except that, viewed more broadly, both can be seen as having Australian and/or wider Indo-Pacific relationships. Both species retain obligate marine connections at least for larval and juvenile life (torrentfish), or they must reproduce at sea (black flounder).

16.6 Why No Similar range Expansions for Retropinnidae and Eleotridae

It might fairly be asked: ‘If galaxiids could spread around the southern cool temperate latitudes by transoceanic dispersal, why have retropinnids or other groups not also done the same?’ Stokell (1953), for instance, expressed some disquiet that *Retropinna* is not present on the Auckland and Campbell Islands well to the south of

New Zealand, where *Gl. brevipinnis* is present. There is no explicit, coherent answer to that question. Biogeography is primarily about elucidating what has happened in the past, rather than speculating about why what didn't happen didn't happen! Stokell's question is a fair one, but not something to 'stumble on.' New Zealand freshwater fish species that are shared variously with southeastern Australia and Tasmania to the west of New Zealand, the Chatham Islands to the east, or through relationships with Auckland and Campbell Islands to the south, and also to Patagonian South America and the Falkland Islands far to the east are, in all instances, diadromous. Just as one of the key elements of freshwater fish distributions within New Zealand is the very widespread latitudinal ranges of the diadromous species resulting from oceanic dispersal (see Chapter 10) – dispersibility seems also to be a significant driver of the even broader geographical ranges around the Southern Ocean. The issue may be a little clearer for the Eleotridae as this family is essentially very widespread indeed across the tropics and sub-tropics (Thacker and Hardman 2005; Nelson 2006), and achieves its most southern range limits and is found in much the coldest habitats in submontane streams of southern New Zealand. There are other issues, as well, that relate to the ability of diadromous fishes on small, isolated oceanic islands to self-recruit back to these islands' fresh waters. Seemingly, one diadromous galaxiid species manages to do this at the Auckland and Campbell Islands, whereas four further diadromous galaxiids, plus diadromous species in all other families found in New Zealand fresh waters don't, and it is perhaps as surprising that one does, as that a variety of others don't. There is no explicit information on where the populations of koaro on these islands recruit from. Similar issues relate to the freshwater fishes of the Chatham Islands, where more species are present, though some diadromous New Zealand species are not present there (see [Section 17.34](#)).

16.7 Percichthyids Perhaps also Once Present

Fossil evidence shows that there were once also freshwater percichthyid fishes, or similar, present in New Zealand – based on fossil scales from the Miocene of Central Otago (about 20 million years ago: McDowall and Lee 2005). These two rather pathetic scale fragments (see Fig. 1.12, p. 24) are with little doubt the most significant freshwater fish fossils known from New Zealand in terms of the revelation of a novel component in the fauna. Freshwater percichthyids are also known from Australia and Patagonian South America (Jerry et al. 2001; Faulk et al. 2009), so perhaps the group is another one that has quite ancient Gondwanan relationships. But the possibility of dispersal cannot be ignored, and some Australian percichthyids are diadromous (Harris 1986; Harris and Rowland 1996).

Studies of the phylogenetic relationships of percichthyids in southern lands are needed to resolve biogeographical issues involving Australia, Patagonian South America, and now New Zealand, though the place of this putative New Zealand percichthyid is unlikely to ever be resolved with any clarity unless much more and better fossil material is discovered.

References

- Avice JC (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA, 464 pp
- Avice JC (2009) Phylogeography: retrospect and prospect. *J Biogeogr* 36:3–15
- Ball IR (1975) Nature and formulation of biogeographical hypotheses. *Syst Zool* 24:407–430
- Brown JH, Lomolino MV (1998) *Biogeography*. Sinauer, Amherst, MA, 691 pp
- Burridge CP (2002) Antitropicality of Pacific fishes: molecular insights. *Environ Biol Fish* 65:151–164
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 238 pp
- Campos H (1984) Gondwana and neotropical galaxioid fish biogeography. In: Zaret T (ed) *Evolutionary ecology of neotropical freshwater fishes*. Junk, The Hague, The Netherlands, pp 113–125
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Craw RC (1979) Generalized tracks and dispersal in biogeography: a response to RM McDowall. *Syst Zool* 28:99–107
- Craw RC (1989) New Zealand biogeography: a panbiogeographic approach. *N Z J Zool* 16: 527–547
- Craw R, Heads MJ, Grehan JR (1998) *Panbiogeography: tracking the history of life*. Oxford University Press, New York, 229 pp
- Croizat L, Nelson GJ, Rosen DE (1974) Centers of origin and related concepts. *Syst Zool* 23:265–287
- du Reitz GE (1940) Problems of bipolar plant distributions. *Acta Phytogeog Suecica* 13(224):240–256
- Ebach M, Humphries CJ, Williams DM (2003) Phylogenetic biogeography deconstructed. *J Biogeogr* 30:1285–1296
- Endler JA (1982) Problems in distinguishing historical from ecological factors in biogeography. *Am Zool* 22:441–452
- Faulk LK, Gilligan DM, Beheregaray LB (2009) Evolution and maintenance of divergent lineages in an endangered freshwater fish *Macquaria australasica*. *Cons Gen* DOI. doi:10.1007/s10592-009-99376-7
- Fink W (1984) Basal euteleosts: relationships. *Am Soc Ichthyol Herpetol Spec Publ* 1:202–206
- Flannery T (1984) New Zealand: a curious zoogeographic history. In: Archer M, Clayton G (eds) *Vertebrate zoogeography and evolution in Australasia (animals in space and time)*. Hesperian Press, Carlisle, NSW, pp 1089–1094
- Fulton W (1986) The Tasmanian mudfish. *Fish Sahul* 4:150–151
- Gibbs GW (2006) *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton, Nelson, N Z, 232 pp
- Gill HS, Renaud CB, Chappleau F, Mayden RL, Potter IC (2003) Phylogeny of living parasitic lampreys (Petromyzontiformes) based on morphological data. *Copeia* 2003:687–703
- Harris JH (1986) Reproduction of the Australian bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae) in the Sydney Basin. *Aust J Mar Freshwater Res* 37:209–235
- Harris JH, Rowland SJ (1996) Australian freshwater cods and basses. In: McDowall RM (ed) *Freshwater fishes of Southeastern Australia*. Reed, Chatswood, NSW, pp 150–163
- Hubbs CL (1952) Antitropical distributions of fishes and other organisms. *Proc 7th Pac Sci Congr* 3:324–329
- Humphries CJ, Parenti LR (1999) *Cladistic biogeography: interpreting patterns of animal and plant distributions*, 2nd edn. Oxford University Press, Oxford, 187 pp
- Jerry DR, Elphinstone MS, Baverstock PR (2001) Phylogenetic relationships of Australian members of the family Percichthyidae inferred from mitochondrial 2srRNA sequence data. *Mol Phyl Evol* 18:335–347

- Johnson GD, Patterson C (251) Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic, New York, pp 251–332
- Kodandaramaiah U (2009) Vagility: the neglected component in historical biogeography. *Evol Biol* 36:327–355
- McCarthy D, Ebach MC, Morrone JJ, Parenti LR (2007) An alternative Gondwana: biota links South America, New Zealand and Australia. *Biogeografia* 2:2–12
- McDowall RM (1964) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1980) Freshwater fishes and plate tectonics in the south western Pacific. *Palaeogeog, Palaeoclim and Palaeoecol* 31:337–351
- McDowall RM (1990) New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1997) Affinities, generic classification, and biogeography of the Australian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Rec Aust Mus* 49:121–137
- McDowall RM (2000) Biogeography of southern cool temperate galaxioid fishes: evidence from metazoan macroparasite faunas. *J Biogeogr* 27:1221–1229
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McDowall RM (2008) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM, Lee DE (2005) Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *J R Soc N Z* 35:339–344
- McDowall RM, Waters JM (2004) Phylogenetic relationships in a small group of diminutive galaxiid fishes and the evolution of sexual dimorphism. *J R Soc N Z* 34:23–37
- McDowall RM, Whitaker AH (1975) The freshwater fishes. In: Kuschel G (ed) *Biogeography and ecology in New Zealand*. Junk, The Netherlands pp 277–299
- McGlone MS, Duncan RP, Heenan PB (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J Biogeogr* 28:199–216
- McLoughlin S (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Am J Bot* 49:271–300
- Michaux B (2000) Island life: millennium book review number 1. *J Biogeogr* 27:219–222
- Mildenhall DC (1980) New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeog, Palaeoclim, Palaeoecol* 31:197–233
- Miles NG, West RJ, Norman ND (2009) Does otolith chemistry indicate diadromous life cycles for five Australian riverine fishes? *Mar Freshwat Res* 60:904–911
- Nelson JS (2006) *Fishes of the world*, 4th edn. Wiley, New York, 601 pp
- Oppen MJH, Olsen JL, Stam WT, van den Hoek C, Wiencke C (1993) Arctic-Antarctic disjunctions in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridis/willii* (Phaeophyta) are of recent origin. *Mar Biol* 115:381–386
- Riddle BR (2009) What is modern biogeography without phylogeography. *J Biogeogr* 36:1–2
- Rosen DE (1974) Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. *Bull Am Mus Nat Hist* 153:265–326
- Schuster RM (1969) Problems of antipodal distributions in lower land plants. *Taxon* 18:46–91
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123

- Stokell G (1953) The distribution of the family Galaxiidae. *Proc 7th Pac Sci Congr* 4:48–52
- Thacker CE, Hardman MA (2005) Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidi). *Mol Phyl Evol* 37:858–871
- Waters JM, Burrridge CP (1999) Extreme intraspecific mitochondrial DNA sequence divergence in *Galaxias maculatus* (Osteichthys: Galaxiidae), one of the world's most widespread freshwater fish. *Mol Phyl Evol* 11:1–12
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, Wallis GP (2001) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Dijkstra LH, Wallis GP (2000) Biogeography of a Southern Hemisphere freshwater fish: how important is marine dispersal? *Mol Ecol* 9:1815–1821
- Waters JM, White RWG (1997) Molecular phylogeny and biogeography of the Tasmanian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Aust J Zool* 45:39–48
- Waters JM, Saruwatari T, Kobayashi T, Oohara T, McDowall RM, Wallis GP (2002) Phylogenetic placement of retropinnid fishes: data set incongruence can be reduced by using asymmetric character state transformations. *Syst Biol* 51:432–449
- Williams RWG (1997) Bones and muscles of the suspensorium in the galaxioids and *Lepidogalaxias salamandroides* (Teleostei: Osmeriformes) and their phylogenetic significance. *Rec Aust Mus* 49:139–166

Chapter 17

Biogeographical Synthesis: 2. More Local Issues and Patterns

Abstract At the more local level, patterns of distribution of the non-diadromous species in the fauna relate to a long series of events that relate to New Zealand's geological and climatic history: beginning with New Zealand's substantial, some think complete, marine submergence in the Oligocene; deposition of fossils in Miocene lakes of Central Otago; the implications of the Alpine Fault, submergence of the southern North Island in the Pliocene; widespread Miocene to Recent volcanism; a series of localised river catchment changes in diverse river systems; Pleistocene glaciation; and the presence of species on the distant Chatham, Auckland and Campbell Islands to the east and south of mainland New Zealand. Speciation processes and distribution patterns were influenced by all of these processes and events.

Keywords Isolated oceanic islands • Glaciation • Marine submergence • Miocene • Pleistocene • Pliocene • River drainage patterns • Speciation • Volcanism

17.1 An Ancient Fossil Fish Fauna

There was once what seem to have been taxonomically modestly-rich fish faunas in New Zealand palaeo-lakes in the Miocene. These include the unidentified, but quite possibly largish, scaled lower perciform fish from near Bannockburn in Central Otago (McDowall and Lee 2005) (see Figs. 1.12, 1.13). There was a clearly distinct species of *Galaxias* from a Miocene palaeo-maar lake near Middelmarsh, described as *Gl. effusus* by Lee et al. (2007: see Fig. 1.10). Also, there was another seemingly distinctive galaxiid (McDowall and Pole 1997); as well, other galaxiids whose fossils cannot be distinguished from koaro and/or extant members of the *G. vulgaris* species complex (McDowall 1976); also unidentified eleotrid(s) but perhaps a *Gobiomorphus* (McDowall et al. 2006b). Many of these were present in Palaeo-Lake[s] Manuherikia in the Miocene of Central Otago. This was an extensive, perhaps shallow water body (or perhaps there were several lakes), with area estimated as >5,600 km² (Douglas 1986; Lee and Forsyth 2008), and so it was of substantial size (amongst the 30 largest lakes in the world, according to Berra's (2007) list.

There were also probably eleotrids (McDowall et al. 2006b; Kennedy and Alloway 2004; Kennedy et al. 2008) and a *Prototroctes* grayling in a Pleistocene lake at Ormond, inland from Gisborne in Poverty Bay in the northeastern North Island (Oliver 1928; McDowall et al. 2006a). Thus, it can be imagined that the freshwater fish fauna of New Zealand lakes though the Cenozoic could once have been more diverse than, and probably very different from, what it now is.

Of some relevance to the above, is a comment by Daugherty et al. (1993) that extant taxa more generally associated with lakes tend to be depauperate in contrast with modern stream faunas. This need not have been true of the mid-Cenozoic New Zealand freshwater fish fauna nor, for that matter, of other taxonomic groups. Modern lakes in New Zealand seem to have brief lives (certainly the existing lakes are thought usually to be very young – Lowe and Green 1987, 1992), and they tend to become physically isolated water bodies. Also, perhaps there has been more rapid turnover of fish populations in lake-adapted taxa compared with those of rivers, especially because the lakes themselves tend to be more ephemeral. This does not, of course, mean that ancient Cenozoic lakes were as youthful and evanescent as modern ones seem to be. It is true, now, that lakes (apart from a few lowland, saline lakes like Lakes Onoke/Wairarapa and Ellesmere), have rather sparser freshwater fish faunas than rivers, for the same reason – they are geologically young, and there are few fishes that are lacustrine endemics. This may not always have been so, and the relatively little information that we have on fossil fish faunas points to likely higher ancient diversity of lake fishes than at present. Present fish diversity in lakes is, once more, largely a product of the presence of diadromous species.

In contrast, New Zealand's palaeo-river fish fauna is totally unknown and is likely to remain so.

17.2 Long Time-Scale Processes in the Biogeography of the Fauna

Assuming that there were freshwater fishes present in Zealandia, prior to its detachment from Gondwana around 80 million years ago (and that seems an entirely reasonable assumption), the existing fauna has had the opportunity to evolve and to accumulate over very long time-scales, probably throughout the Cenozoic – unless, however, New Zealand became entirely submerged by sea, as some geologists and biologists are suggesting (Trewick et al. 2007; Campbell and Hutching 2007; Landis et al. 2008). If there were the sorts of smallish residual Oligocene islands hypothesised by Fleming (1979) (see Fig. 3.2) they may have had quite diverse freshwater fish faunas based in each. That question aside, whether, and to what extent, the fauna present today is derived from an ancient Gondwanan/New Zealand ancestry, or from the somewhat later, known, fossil fauna, is uncertain; possibly there is some of both of these. If a Gondwanan ancestry is evident anywhere, still, it may be in the pencil-galaxias species group, the ancestry of which remains uncertain (McDowall and Waters 2002, 2003), and for which there are no certain, or

explicitly hypothesised, genealogical linkages to either known fossils or to other elements in the existing faunas of fresh waters. Study is needed at a broad, Southern Hemisphere-wide scale. Other contemporary groups, however, appear to have quite close relationships among diadromous fish groups outside New Zealand and an explicit or exclusive Gondwanan connection is unlikely.

I have long argued that rather than having a direct Gondwana ancestry, much of the New Zealand freshwater fish fauna instead probably has dispersal origins (McDowall 1964, 1969, 1978, 2002, 2008), and consistent with this is the very recent arrival of the diadromous Australian spotted eel in the New Zealand fauna (McDowall et al. 1998). In addition, derivations of some of the contemporary fauna indicate local marine origins (torrentfish, black flounder). Otherwise, existing evidence suggests that the non-diadromous component of the present fauna results, substantially, from repeated, parallel losses of diadromy, leading to the establishment of locally-endemic non-migratory species that became reproductively isolated from their diadromous congeners in New Zealand rivers and lakes (McDowall 1972, 1990; Waters and Wallis 2001a; Stevens and Hicks 2009). The biogeographical details of the processes involved in this historical shift are largely not understood, but they could have involved the existence of the Miocene lake(s) in Central Otago (discussed above, and see Douglas 1986), from where many of the older reported New Zealand freshwater fish fossils came (McDowall 1976; McDowall and Pole 1997; McDowall and Lee 2005; McDowall et al. 2006a, b; Lee et al. 2007).

17.3 The Implications of New Zealand's Residual Islands in the Oligocene

Probably the oldest of the identifiable macro-scale geological/historical influences on New Zealand's freshwater fish fauna (as well, perhaps, as on its whole biota: Cooper and Cooper 1995), apart from its former connections with Gondwana, was the purported Oligocene reduction of the emergent land area of New Zealand to, at most, several small islands almost certainly with cumulative land area less than 20% of the present area (Fleming 1979; Cooper and Millener 1993: see Fig. 3.2) though, as already noted, some observers have broached the possibility of total submergence (Campbell and Landis 2005; Campbell and Hutching 2007; Landis et al. 2008). Some other biotic elements now present in New Zealand may suggest that there was always some emergent land, especially some obligate freshwater taxa such as the freshwater parastacid crayfish genus *Paranephrops*, its associated temnocephalid commensals; or the freshwater mussel *Echyridella*, and this would have required the presence of a freshwater fish for the parasitic larval glochidial stage; the insect *Nannochorista* (Gibbs 2006); freshwater phreatoicid crustaceans (Wilson 2008); the mite harvestmen (Boyer et al. 2007; Boyer and Giribet 2009) and no doubt other groups for which there are not well-developed phylogenetic scenarios, such as peripatus, turbellarians, annelid worms, freshwater leeches, and

other poorly known groups could also be mentioned. The survival in New Zealand of the Acanthisittidae (the endemic wrens) is another interesting case. These tiny birds are now recognised as basal to all passerine birds (Ericson et al. 2002), and this ancient connection to bird evolution creates a scenario that would seem to demand some land present in New Zealand continuously since the Cretaceous (or some rather elaborate, and perhaps unlikely, alternative biogeographical scenario).

The freshwater hyridellid mussels are another interesting case. Graf and O'Foighil (2000) have suggested that the hyridellid mussels are an ancient, Gondwanan group, that molecular "branch lengths were consistent with Mesozoic vicariance and that the Hyriidae pre-date the break-up of Gondwanaland". On this basis they argue that "the New Zealand Hyridellini are relics rather than colonizers". Thus, on the basis of molecular studies, Graf and Cummings (2007) re-affirmed the ancient connections of this group of molluscs to New Zealand's ancient history, and argue for the group's very early heritage. Two genera are shared between Australia and New Zealand, and so there are dual connections, perhaps increasing the likelihood of their ancient Gondwanan presence. Walker et al. (2001) allowed for the prospect of transoceanic dispersal of this freshwater mussel by the parasitic glochidial life stage attached to diadromous anguillid eels that are shared between Australia and New Zealand, but this is simply preposterous: there is no hint of evidence that adult eels move between these two lands, and any dispersal of *Anguilla* seems much more likely to involve oceanic spread of the leptocephalus larvae upon which the attachment of glochidia is impossible, since anguillid leptocephali are never found in fresh water, and so could not pick up glochidia. Moreover, it is highly uncertain that the glochidia attached to adult eels could survive the long-term immersion in sea water that would be necessary for any such dispersal. Haas (1969) reported freshwater mussels as early as the Triassic, so their occurrence on Gondwanan seems fairly certain.

Nothing observable in the diversity or distributions of the present New Zealand freshwater fish fauna, explicitly suggests that patterns in the distributions of the diadromous fish species retain even residual vestiges of any of the hypothesised Oligocene residual islands – presumably substantially owing to the ease with which the fauna of diadromous species can spread around New Zealand through the sea (discussed at length elsewhere). There seems to be continual dispersal going on through coastal seas around New Zealand (Barker and Lambert 1988; Allibone and Wallis 1993), at least as indicated by the lack of genetic structuring in fishes like the New Zealand inanga, and similarly, also New Zealand's freshwater anguillid eels (Dijkstra and Jellyman 1999; Smith et al. 2001), which have been shown to exhibit little or no genetic structuring across their very broad, virtually New Zealand-wide geographical ranges. Dispersal will undoubtedly have obliterated any residual effects of the Oligocene submergence and other disruptions of the geology of the New Zealand land mass on the diadromous component of the freshwater fish distributions, and any residual effects of the hypothesised submergence on the distributions of freshwater fish would therefore be evident only in the distributions of the non-diadromous fraction of the fauna.

The fact that the location of the richest existing diversity of non-diadromous freshwater fishes in New Zealand, is in Otago/Southland, is perhaps a heritage of

that area being derived from the purported major emergent landscape persistent in New Zealand in the Oligocene, if there was any emergent land at that time; any such land would be amongst the most ancient New Zealand landscapes known (see Fig. 3.2). Nevertheless, we can probably expect to discover little, in relation to that Oligocene landscape, of the processes that have affected the ancient distributions of these fish species, because so much of the landscape of southern New Zealand has changed since then (reviewed in Craw and Norris 2003). However, there are several scenarios in which some of the Cenozoic history can perhaps be seen.

Even though the presence in New Zealand of the pencil-galaxias species complex could derive from such an ancient Gondwanan heritage (but only if there was some continuous land since the Cretaceous), there is little explicit indication of an ancient history in the diversity and distribution of that species complex, except perhaps for the minor radiation in the Mackenzie Basin of the Waitaki River, where there are four pencil-galaxias species present (see Fig. 12.3), and this area could have ancient connections to the emergent, southern Oligocene landscape (either through or following the period of Oligocene submergence). Some molecular evidence has been interpreted as suggesting that divergence of the upland and lowland longjaw galaxias may date back as far as the Miocene (McDowall and Waters 2002), although more recent molecular data are suggesting that divergence in New Zealand galaxiids may be rather faster than hitherto thought (Craw et al. 2008).

Any other hypothetical New Zealand Oligocene islands whose land surfaces survive to the present time are thought to have been much smaller than the southern one (see Fig. 3.2: Fleming 1979), and there is no hint that any of the existing freshwater fish diversity sprang from these – though it could have. One of the other hypothesised Oligocene ‘islands’ (Fleming 1979) equated roughly to the present-day Coromandel Peninsula in northeastern North Island (see Fig. 3.2, arrow 1), where there are now virtually no non-diadromous fish species at all – just two records of Cran’s bully in the Whangarahi Stream in Coromandel Harbour (see Fig. 15.2, arrow 17), despite widespread stream sampling in the area.

17.4 Implications of the Alpine Fault

One of the dominating geological processes that has contributed to the shape of the contemporary New Zealand landscape has been the divergent, bilateral displacement of land areas to the east and west of the New Zealand Alpine Fault (see Section 3.6). This has profoundly affected the shape and geographical associations of much of the New Zealand landscape through most of the Cenozoic. Distinctive ultramafic geological formations in northwest Nelson and far South Westland, which are believed to have shared early Cenozoic conjoined, geological origins, have become separated by bi-lateral displacement of ca. 480 km northwest and southeast of the Alpine Fault over the last 25 million years, and this movement continues in the present day (Kamp 1992a; Whitehouse and Pearce 1992; Craw and Norris 2003; Campbell and Hutching 2007; Bradshaw and Soons 2008). As far as I have been

able to determine, little if any biogeographical heritage associated with the Alpine Fault can be discerned in the existing distributions of freshwater fish – unless it is in the sparseness or absence of populations of non-diadromous species in the northwestern South Island (there are no records of dwarf galaxias and few of upland bullies west of the Fault). However, these species are widely present in the north-eastern South Island across Nelson-Marlborough, and are widespread west of the Alpine Fault to the south, in the Buller, Grey, Taramakau and Hokitika River catchments; thus their distributions seem to bear little or no relation to landscape displacement along the fault. The Southern Alps themselves appear to have been much more influential on patterns of distribution and diversity than the fault itself has. Some rather more minor fault activity in inland Marlborough is thought to have had implications, discussed above, for the history of the Tarndale bully (see Chapter 15), though this does not relate explicitly to major movement in the Alpine Fault, and is relatively recent (c. 18,000 years – Bowen 1964; McAlpin 1992).

Thus, contemporary freshwater fish distribution patterns appear to have developed across a landscape that is much more recent than that influenced by the major movement of the Alpine Fault. Nothing comparable to what was hypothesised by Heads (1998) as an outcome of the fault for diverse faunal elements is evident in the fish fauna; moreover, Heads' (1998) ideas were thoroughly scotched by Wallis and Trewick (2001) – though Heads seems to have thought otherwise (Heads and Craw 2004). The re-emergence and re-inhabitation of terrestrial and freshwater landscapes/habitats following the Oligocene submergence means that there must have been extensive, major, and widespread redispersal of any biota that survived the Oligocene, anyway. Any residual effect that may have reflected the original juxtaposition of the lands before the movement involved in the Alpine Fault will have been largely obliterated.

17.5 The Evolution of an Alpine Biota

The relative youth of the mountain ranges of New Zealand (late Cenozoic) means that there had, hitherto to their uplift, been no significant mountain biota in New Zealand since the Cretaceous (discussed generally for New Zealand in Section 3.8). The Miocene landscape of New Zealand is usually described as having had no significant mountain ranges, and being of 'low relief' with a warm-temperate climate (Lee et al. 2001; Campbell and Hutching 2007). The recognition that New Zealand generally lacked an alpine terrestrial biota during the early-mid Cenozoic has not hitherto included discussion of the freshwater fish fauna, though clearly there is an implication that those fish species now found at higher elevations, such as alpine galaxias and upland longjaw galaxias may have evolved, or have at least become sub-alpine/alpine, relatively recently, perhaps in association with uplift of the Southern Alps from Pliocene to Recent times. Certainly, they must have achieved their higher-elevation distributions quite recently, since most of the areas where they are now present were ice-covered in the Pleistocene (see discussion of

Tarndale bully in [Section 15.2](#)). It seems quite likely, too, that the present alpine fauna and flora evolved during the Pleistocene glaciations when not only were the mountains increasing in elevation but there were also colder climates as well ([Wardle 1963, 1968, 1978](#); [Mark and Adams 1973](#); [Winkworth et al. 2005](#); [Gibbs 2006](#); [Campbell and Hutching 2007](#); [Burrows and Wilson 2008](#)).

The biota that now occupies the alpine zone seems likely to have retreated to these higher elevations, from the lowlands, as climate ameliorated during the Pleistocene, especially in the South Island – partly post-glacial because ambient temperatures became more congenial for cold-adapted taxa at higher elevations, and partly because alpine habitats upslope were becoming accessible to invasion as the ice retreated, i.e. species may have become cold-tolerant at low elevations during glacial advances (climatic cooling) and, if so, this preadapted them to occupying the alpine habitats as climate cooled, and higher elevation sites became available/inhabitable. If species were stenothermal, as well as cold-adapted, they would have had to retreat into the mountain valleys (as is probably particularly true of upland longjaw galaxias). Thus the fishes now occupying the streams and rivers of the intermontane valleys of the eastern South Island may have evolved out on the plains and have penetrated upstream into the valleys as climates warmed and as glaciers retreated. Not everything shifted: On the one hand, Kauru River populations of lowland longjaw galaxias, discussed above (see [Section 12.5](#)), were ‘left behind’ at low elevations following this retreat; on the other, upland longjaws for some reason failed to reinvade the Waimakariri River catchment at all ([Section 12.4](#)), though other species did, such as Canterbury galaxias ([Section 11.2.2](#)), alpine galaxias ([Section 12.2](#)) and upland bully ([Section 15.3](#)). It is of interest that in the South Island, the non-diadromous fauna is very largely on the eastern flanks of the Southern Alps, especially at mid- and southernmost latitudes, this perhaps being due in large measure to the influence of glaciation in the west. There is no hint of a distinctive alpine freshwater fish fauna to the west of the Southern Alps except perhaps the modest diversity in the Maruia River, in the headwaters of the Buller River, near the Lewis Pass (discussed in Chapters 11 and 12). However patterns of fish distribution there must have been greatly influenced by events during the Pleistocene glaciation, and may reflect these events more than they do patterns of phylogenetic relationships and connections.

17.6 Pliocene Submergence and Then Re-emergence of the Southern North Island

An extensive southern sector of the present North Island was submerged beneath sea during the Pliocene ([Fleming 1979](#); [Whitehouse and Pearce 1992](#); [Lewis and Carter 1994](#); [Lewis et al. 1994](#); [Fig. 3.3](#)); this must, of course, have had profound biogeographical implications for terrestrial biota, including freshwater fishes – to the extent that any fish now present in the southern North Island must have spread there since that land again become emergent and there were riverine habitats

present there. Chapple et al. (2009) refer to this as the “Taupo line”. As discussed above (Section 15.3), the southern North Island is an area where there is interesting broad overlap of upland and Cran’s bullies (see Fig. 15.2, arrow 14; Fig. 15.5) – perhaps an outcome of the re-emergence of that area from the sea, followed by invasion from the south by upland bully and from the north by Cran’s bully. The widespread presence in the southern North Island of dwarf galaxias (see Fig. 12.2 – blue symbols, arrow 3) and brown mudfish (see Fig. 14.3 – brown symbols, arrows 13 and 14) presumably also relates to their similar re-occupation of this area since retreat of the sea, though from what direction they did so is unclear (this might eventually be revealed by molecular sequencing studies). It is conceivable that a small peninsula of land that connected an area of the southern North Island to the northern South Island (see Fig. 3.3) held freshwater fish species, such as dwarf galaxias, brown mudfish and upland bully, which later spread more widely in the southern North Island, as it emerged from the sea, though this would be difficult to corroborate. The northern limits of upland bully in the southern North Island (see Fig. 15.2 – blue symbols, arrow 14) are quite similar to the northern limits of the North Island areas submerged during the Pliocene (see Fig. 3.3), and this fish tends to be present in those southern North Island catchments that may once have been confluent with northern South Island catchments when sea levels were lower and Cook Strait was bridged by land. Fine details aside, there must, again, have been massive amounts of re-dispersal to populate the landscapes of the southern North Island after they emerged from the sea, and/or were built up by erosion of mountain ranges as they rose, though the geological history is very complex (Kamp 1992b, c; Eyles and McConchie 1992). However, even though the northern range limits of upland bully may coincide to some extent with the land area south of Chapple et al.’s (2009) Taupo line, this seems likely to be coincidental, and I can find no freshwater fish distributions that seem attributable specifically to the submergence of the southern half of the North Island. No species exhibits a southern range limit that seems attributable to the land that remained emergent through the Pliocene and all non-diadromous fish species that are present north of the Taupo line also extend south of the line and as far south as Cook Strait.

17.7 Occupation of the Aupouri Peninsula in the Far North

The waterways on the Aupouri Peninsula in far northern New Zealand only became available for freshwater fish, as a sand tombolo established a connection between a formerly isolated island in the far north and the main body of Northland during the Pleistocene, according to Brook (1999) (see Fig. 3.3). The non-diadromous freshwater fish fauna of this area is sparse. Black mudfish has been able to occupy the waterways of the peninsula (see Fig. 14.3, arrow 1), but Cran’s bully, the only other widespread far-northern non-diadromous freshwater fish species, has not (see Fig. 15.2, arrow 1). Molecular study is needed to ascertain whether the far northern population of black mudfish, near Parengarenga Harbour (see Fig. 14.3, arrow 1) was there prior to

connection of the Aupouri Peninsula to Northland, or spread north along the peninsula since land connection by formation of the tombolo. This question, too, would be difficult to evaluate.

17.8 Endemism in the Northern North Island

There is some modest localised diversification of freshwater fish in the northern North Island, with dune lakes galaxias (see [Fig. 13.2](#)), black, and burgundy mudfishes (see [Fig. 14.3](#) – arrow 20) being the only non-diadromous species found only in the north. Dune lakes galaxias and burgundy mudfish appear to be examples of distinctive, highly-localised speciation processes. Dune lakes galaxias is clearly a locally-evolved, non-diadromous, lacustrine derivative of the diadromous inanga. Speciation processes leading to burgundy mudfish are not understood.

17.9 Volcanism in the Auckland Isthmus

Prolonged and widespread volcanism in the Auckland isthmus (discussed in [Section 3.5](#)) does not seem to be reflected in freshwater fish distributions. Cran's bully is common and widespread though this area (see [Fig. 15.2](#), arrow 18), and black mudfish has recently been found there, though rarely (see [Fig. 14.3](#), arrow 19). Intensive anthropogenic effects related firstly to volcanism, later to ancient Polynesian Maori inhabitation, and then more recently the large and dense human population of the area and the modern city of Auckland and associated/contiguous metropolitan cities, may well have overwhelmed any residual biotic effects on stream fishes relating to that Holocene volcanism. Diadromous species are widespread there and undoubtedly this results from continual dispersion through coastal seas following recovery from perturbation resulting from volcanism or any other adverse impacts. The diadromous banded kokopu is surprisingly abundant and widespread across this region, given the intensive human development of this area and a perception that banded kokopu prefer forested streams ([McDowall 1990](#); [Rowe et al. 1999](#)).

17.10 Signs of the Former Manukau Strait Across the Auckland Isthmus

There was once a sea passage, the so-called Manukau Strait, across the Auckland Isthmus, which for a time were isolated Northland from the rest of the North Island ([Ballance and Williams 1992](#)). [Gleeson et al. \(1999\)](#) attributed genetic divergence

between Northland and Waikato populations of black mudfish to the separation created by this seaway, though they did not calibrate the genetic divergence against the hypothesized timing of the timing of that seaway. There is no other existing hint in the distributions of freshwater fishes of any influence of the Manukau Strait at broader-scale taxonomic levels, though molecular studies of Cran's bully may prove interesting. As noted in the previous paragraph, the very intensive urban/human development of this area may have obliterated any residual effects on freshwater fish habitats and distributions.

17.11 Mount Taranaki Volcanism

Catchments draining from all sides of Mount Taranaki, except drainages inland and to the east of the mountain (largely inland reaches of Patea River), consistently lack upland and Cran's bullies, both of which are widespread in the area to the east (inland) of Mount Taranaki (see [Fig. 15.2](#), arrow 3; [Fig. 15.6](#) – blue and red symbols); these western drainages are well-populated by diverse diadromous species, which implies that there are no obvious, persisting habitat-suitability reasons for contemporary absences of non-diadromous species. These absences have the appearance of residual effects of Mount Taranaki volcanism (the most recent eruptions were only 300 years ago: Neall 1992), though brown mudfish is present west of the mountain. The contrast between the presence of brown mudfish on the one hand, and the absence of upland and Cran's bully on the other is interesting. The brown mudfish is a wetland species and its presence in some western waterways may suggest that fluvial habitats were more seriously affected by ash deposition and erosion, than wetland habitats were affected by ash deposition alone, and/or that brown mudfish have been more successful at reinvading these areas than the two species of non-diadromous bully since the effects of volcanism dissipated. There is other evidence that suggests high resilience of brown mudfish in the face of perturbation (see [Sections 14.4 and 17.19](#)).

17.12 Overlapping Distributions in the Mokau River, Northern Taranaki

The southern limits of the range of black mudfish are in the headwaters of the Mokau River in northern Taranaki (see [Fig. 14.3](#), arrow 3; [Fig. 17.1](#) – black symbols) – presumably a heritage of some former fluvial connections between the upper reaches of the Mokau River, and the Waipa River to the east and north where black mudfish is widespread. The northern limits of the distribution of the mostly southern upland bully are also in the headwaters of the Mokau River (see [Fig. 15.2](#); [Fig. 17.1](#) – blue symbols). But, as well, Cran's bully displays a distribution that covers territory substantially to both the north and south of the Mokau River, and so has its own

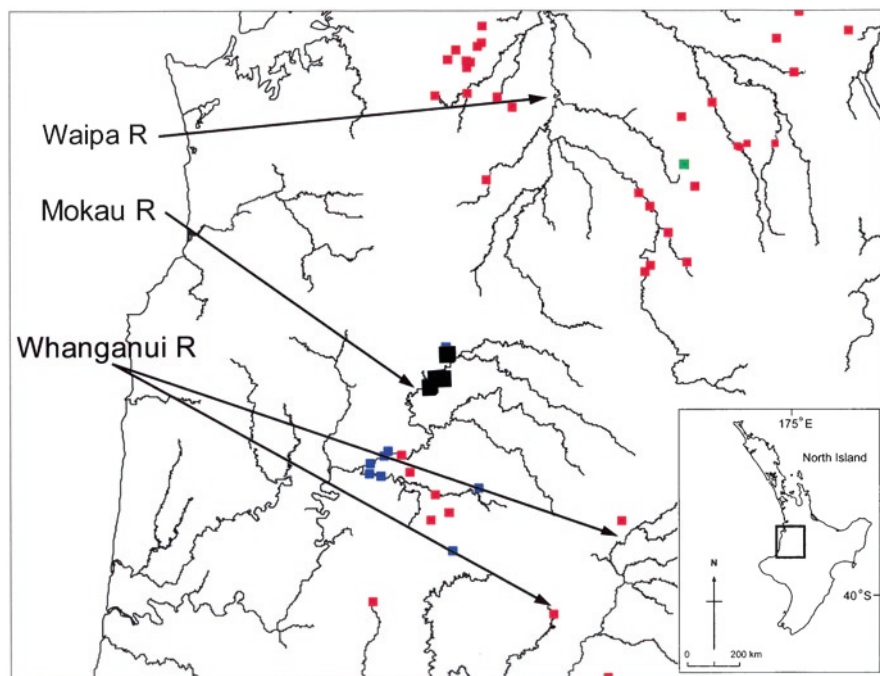


Fig. 17.1 Zone of overlap in the vicinity of the Mokau River in northern Taranaki: black mudfish, *Neochanna diversus* (■); Cran's bully, *Gobiomorphus basalis* (■); upland bully, *G. breviceps* (■). **Arrow:** ↑1: Sites for black mudfish, *Neochanna diversus* in the upper Mokau River; ■ – other sampling sites where none of these species are present

pattern of dispersal across the same landscape. Thus, these three non-diadromous species have distinctive distribution patterns in this area despite there being only a single geological history. Here, then, we see range overlaps of species of northern, southern, and widespread provenance, which shows that distribution patterns have been driven by different dispersal processes resulting in erratic lineage overlaps.

17.13 Impacts of Central North Island Volcanism

The broad absence of non-diadromous species in the central North Island/volcanic plateau, and in the area east- to north-east towards East Cape (dwarf galaxias, see Fig. 12.2, arrows 20; Cran's bully, Fig. 15.2, arrow 16) seems likely to be driven by volcanism, and the resulting ignimbrite and ash deposition, across a wide area and over a long time period (McDowall 1996: see Fig. 3.5). The most recent major, active volcanic eruption was less than c.2,000 years ago (Wilson 1993; Wilson and Houghton 1993), but the area already had a very long, previous, history of intensive,

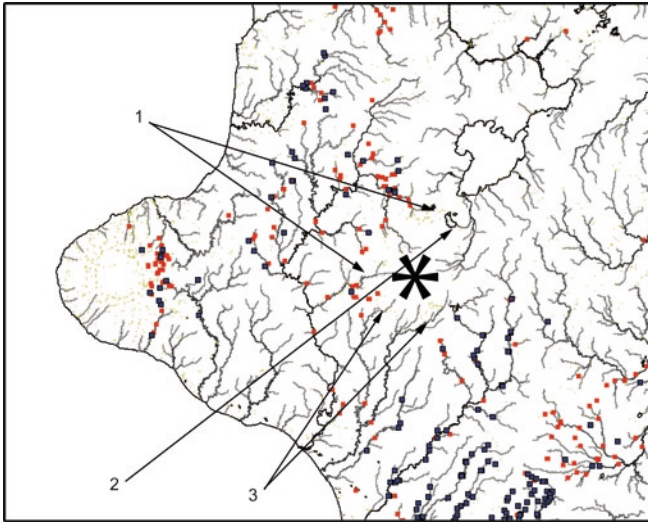


Fig. 17.2 Distributions of non-diadromous species in rivers draining the central North Island volcanoes (★): Cran's bully, *Gobiomorphus basalis* (■); upland bully, *G. breviceps* (■); and numerous sites with no species recorded (■). Arrows – ↑1: upper Whanganui River; ↑2: upper Waikato River, above L. Taupo; ↑3: inland Whangaeahu River

active and repeated volcanism lasting 50,000 years or more. Moreover, there has been some much more recent, if less catastrophic, volcanic activity based in Mounts Tarawera (in 1886), Ruapehu and Ngaruahoe (intermittently in recent decades and continuing: Cole 1970; Clarkson 1990; Healy 1992; Williams and Keys 2008; Anon n.d.).

There are continual discharges of toxic, chemically-contaminated volcanic water from the central North Island volcanoes into rivers radiating in all directions from the slopes of these mountains, and these discharges seem likely to be having ongoing impacts on aquatic fauna that may be best reflected by the impoverished fish faunas, especially in parts of the Whangaeahu River (Deely and Sheppard 1992), and also in some headwater streams of the Whanganui and upper Waikato Rivers that drain west and south off this group of mountains (Fig. 17.2, arrow 1: Tombs 1960; Spiers and Boubée 1997; Edgar 2002). General absence of some fish species, and only fragmentary presence particularly of other non-diadromous fishes, especially in part of the Whangaeahu River (Fig. 17.2, arrow 2), are probably a heritage of repeated discharges of toxic waters from the central North Island volcanoes (Williams and Keys 2008), with these fish, especially Cran's bully, now apparently found quite widely but only in small, isolated pockets. However, widespread presence of some diadromous species of fish across much of the Whangaeahu River suggests continuing immigration of fishes into the river by long-lived species like longfin eels, which have historically formed significant artisanal fisheries for New Zealand's indigenous Maori people (Walzl 2006) – these species have clearly been entering the lower Whangaeahu River from the sea, and have been able to

penetrate the river into those reaches not impacted by continuing volcanism and are present there; moreover, exotic species (rainbow trout, *Oncorhynchus mykiss* and brown trout, *Salmo trutta*) have maintained populations widely across the Whangaehu catchment, so that although volcanism has undoubtedly had periodic and repeated, seriously adverse impacts, these impacts may have been greatly exaggerated, and impacts have been highly local rather than general across this river's catchment: additional sampling across this area is needed.

17.14 Impacts of Rock Types on Contemporary Freshwater Distributions

It is simplistic to attribute broad-scale absences of various non-diadromous fish species, such as pencil-galaxias, mudfishes, and bullies, across parts of the central North Island, entirely, to the impacts of volcanism. There is a degree of coincidence in parts of this same area also having extensive tracts of soft-rock geology. These unmetamorphosed sandstones may have influenced the fluvial fish faunas at the local scale because the waterways draining the landscape tend to have much less coarse, hard rock, cobble substrate – and this has implications for instream cover for fish, many of which live amongst coarse cobble substrates, as do their food organisms. Attention is drawn to the role of these substrates in fish ecologies and distributions by the rather sparse freshwater fish faunas of the rivers of the eastern North Island, from East Cape south to the Wairarapa coast (see [Figs. 9.4a, e, f and Fig. 10.2a, c](#)). Another area of soft rock is in the upper reaches of the Whanganui, Whangaehu and Turakina River valleys (some of which were discussed in the previous paragraph), where there may be coincidental, and perhaps additive, effects of both rock type and volcanism (discharges of toxic waters). This highlights the problem of 'layers of influence' and it is not always clear what layers have been most influential across time and space. This is a question that needs detailed investigation, and the data (New Zealand Freshwater Fish Database) and tools (GIS, molecular analysis) are available to do so. The absence of dwarf galaxias across this broad area is contrary to the widespread presence there of upland and Cran's bullies (see [Section 15.3](#)), so again we see that patterns are inconsistent, and that various groups have their own dispersal processes and patterns.

17.15 Patterns of Presence/Absence in the Wairarapa Area

There are highly contradictory patterns of distribution exhibited by four non-diadromous fish species in the southeastern North Island to the east of the mountain ranges ([Figs. 17.3–17.5](#)). While the patterns are local and idiosyncratic for each species, they also illuminate some general principles applicable to revealing pattern and explaining process. The area from southern Hawkes Bay to the southeastern

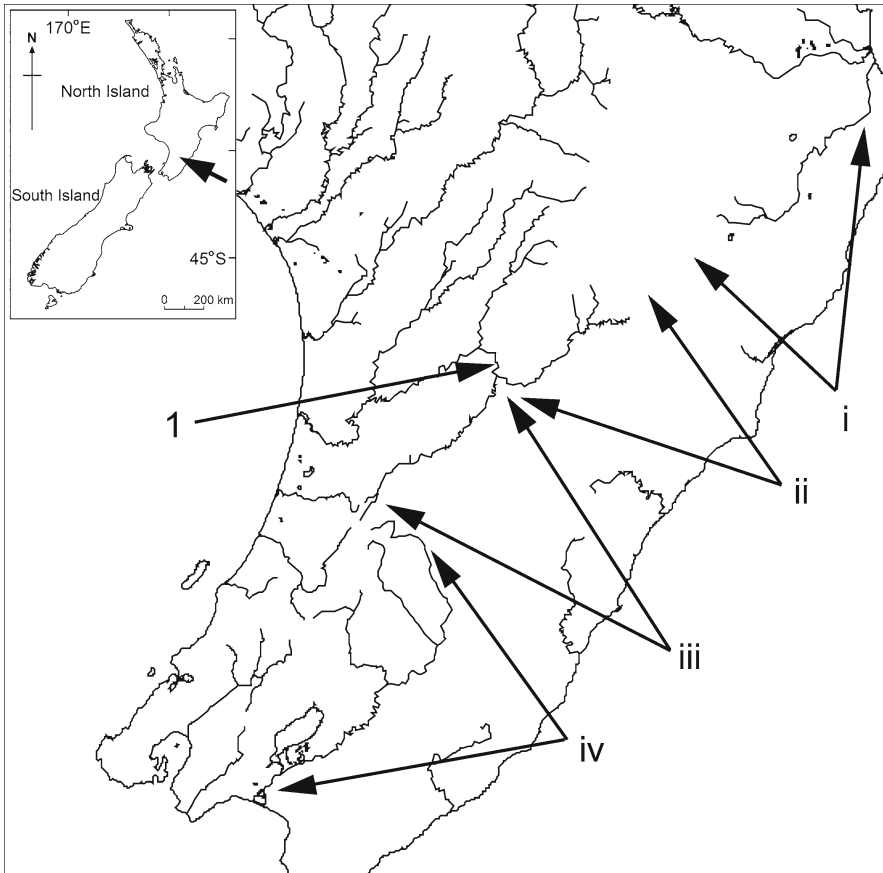


Fig. 17.3 River catchments of the southern Hawkes Bay/Wairarapa, in the southeastern North Island: **i.** southern Hawkes Bay; **ii.** northern tributaries of the Manawatu River; **iii.** southern tributaries of the Manawatu River; **iv.** Ruamahanga River catchment; **↑1:** Manawatu Gorge, through southern North Island mountain range

limits of the North Island, east of the Ruahine and Tararua Ranges, can be subdivided into four major subregions, based on river catchments (Fig. 17.3): viz.

- (i) 'Southern Hawkes Bay' (Ngaruroro and Tukituki Rivers that drain east from the Ruahine Ranges and then north into Hawkes Bay)
- (ii) 'Northern Wairarapa' (northern branches of the Manawatu that primarily drain east off the southern Ruahine Ranges, and then south to, and west through, the Manawatu Gorge)
- (iii) 'Central Wairarapa' (southern branches of the Manawatu River that primarily drain to the east from the eastern flanks of the Tararua Ranges then north to join the north branch of the river, and so, again, west through the Manawatu Gorge)

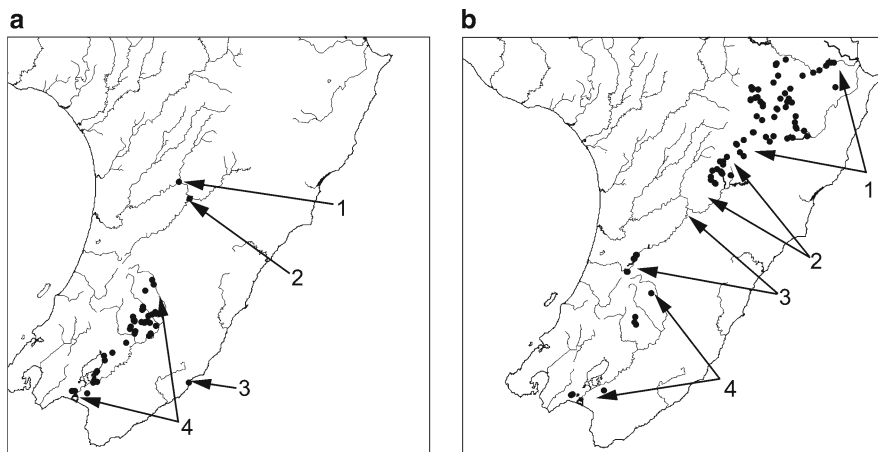


Fig. 17.4 Distinctive distributions of : **a.** Non-diadromous brown mudfish *Neochanna apoda* in the southern Hawke's Bay/Wairapa, in the southeastern North Island – **Arrows** – ↑1: site at western end of Manawatu Gorge; ↑2: a dubious old record at eastern end of Manawatu Gorge; ↑3: an enigmatic coastal site; ↑4: Ruamahanga River; and **b.** dwarf galaxias, *Galaxias divergens*: **Arrows** – ↑1: widespread presence in catchments of southern Hawke's Bay; ↑2: widespread presence in the northern arm of Manawatu River; ↑3: near absence from southern branch of Manawatu River; ↑4: occasional present in Ruamahanga River

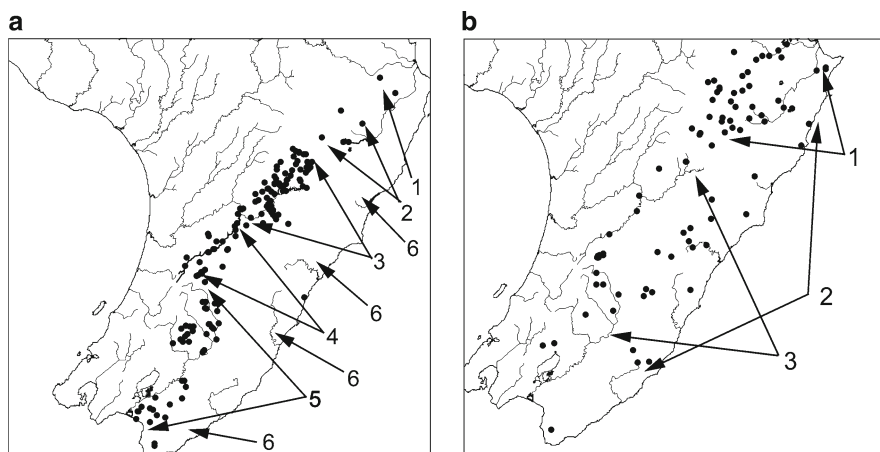


Fig. 17.5 Distinctive distributions of **a.** Upland bully, *Gobiomorphus breviceps* in the of southern Hawke's Bay/Wairapa, in the southeastern North Island. **Arrows** – ↑1: doubtful sites in Hawke's Bay catchments (Ngaruroro and lower Tukituki Rivers); ↑2: absence from most of Tukituki River; ↑3: widespread in north branch of Manawatu River; ↑4: widespread in south branch of Manawatu River; ↑5: widespread in Ruamahanga River; ↑6: rare presence in eastern coastal drainages; **b.** Cran's bully, *Gb. basalis*. **Arrows** – ↑1: widespread occurrence in Hawke's Bay drainages; ↑2: widespread presence in eastern coastal drainages; ↑3: intermittent but widespread presence in both Manawatu and Ruamahanga River drainages

- (iv) ‘Southern Wairarapa’ (rivers draining largely east from the Tararua Ranges and then south via the Ruamahanga River)

It is notable that none of these major Wairarapa rivers catchments drains to the contiguous east coast of the southern North Island, but rather, after draining east off the mountain ranges, they flow either north or south, and then either west via the Manawatu River, or south via the Ruamahanga River (Fig. 17.3). There are a few small, east-flowing coastal drainages along the east coast of the Wairarapa that are independent of the Manawatu and Ruamahanga Rivers (Fig. 17.3). This pattern of drainage is a likely outcome of the area’s complex geological history and, in particular the presence of a quite ancient range of hills along the present east coast with a former narrow, north-south oriented seaway to the west of these hills, and east of the present Tararua Mountain ranges. As sea bed formerly beneath the seaway rose above sea level during the Pliocene, river systems formed that drained the emergent land surface, flowing to the west and south, as now; the west-flowing river (the modern Manawatu), maintained its western connections as the substantial Ruahine and Tararua Ranges became elevated during the Pleistocene, by cutting a deep gorge through the mountains (Kamp 1992b, c) (Fig. 17.3, arrow 1).

In relation to these areas, there are at least four distinct patterns in the distributions of the four non-diadromous fish species known from the area, the details of which are as follows:

- i. Brown mudfish is present primarily in ‘southern Wairarapa’ in streams and wetlands associated with the south-flowing Ruamahanga drainage (see Fig. 14.3, arrow 13; Fig. 17.4a, arrow 4), apart from: two records, one at each end of the Manawatu Gorge (Fig. 17.4a, arrows 1 and 2), though that at the eastern end (arrow 2) is dubious; there is also a rather disjunct record on the coast that appears highly anomalous and is presently biogeographically inexplicable (Fig. 17.4a, arrow 3).
- ii. Dwarf galaxias is widespread in both ‘southern Hawkes Bay’ and ‘northern’ and ‘southern Wairarapa’ (see Fig. 12.2; Fig. 17.4b, arrows 1 and 2); however, it is in only the northern-most headwaters of the ‘northern Wairarapa’ arm of the Manawatu River (Fig. 17.4, arrow 2), and is in general absent from ‘central Wairarapa’ (Tararua tributaries of the Manawatu River – arrow 3) apart from a couple of localities in the southernmost headwaters of the Manawatu (Mangahao River – Fig. 17.4b, the lower of the twin arrows labelled 3); a few populations are also known from the Ruamahanga, to the south (arrow 4) (and these suggest a need to examine the prospect of a former local headwater connection between the uppermost Ruamahanga) and the Mangahao River; however, reasons for this species’ absence from all but the headwaters of the southern arm of the Manawatu River are obscure, unless they can be attributed to the recent impacts of invasion by brown trout (Hopkins 1971).
- iii. Upland bully is generally widespread across ‘northern’, ‘central’ and ‘southern’ Wairarapa, and so is much more widespread than dwarf galaxias; it is in both north and south-draining branches of the Manawatu River (Fig. 17.5a, arrows 3

and 4), as well as in the Ruamahanga River further south (Fig. 17.5a, arrow 5); in addition, there are several localities in the ‘southern Hawkes Bay’ area – in the Ngaruroro and lowermost Tukituki Rivers, and a small, coastal catchment between them (Fig. 17.5a, arrow 1), and these populations raise the prospect of some undescribed riverine connections (or, perhaps, further misidentifications, especially given the widespread presence in these more northern river systems of Cran’s bully, and the absence, otherwise, of *Gb. breviceps* in southern drainages of the Tukituki River) (Fig. 17.5a, arrow 2). A re-collection of fish from one these more northern sites showed the fish there to be *Gb. basalis* rather than *Gb. breviceps*, as originally listed. There is also general absence of upland bully from the small coastal Wairarapa drainages (Fig. 17.5a, arrow 6 – just one record along the coastline that seems aberrant), and this is of interest (or perhaps a dubious identification).

- iv. Cran’s bully is widespread in southern Hawkes Bay, but also is found widely, but intermittently, throughout the northern, central and southern Wairarapa (Fig. 17.5b, arrow 3), including distinctive presence in several of the small coastal drainages (Fig. 17.5b, arrow 2), a marked contrast with upland bully.

Additional work is needed at fine scale to explore these distributions and promote reliable synthesis, partly to ensure the accuracy of identifications, but also to address some aspects of the distributions that look obviously discordant. In the meantime, it appears as though we are dealing here with several different dispersal/landscape processes governing the distributions of each of these four non-diadromous species across a single landscape. Some of the disparity may be due to issues of habitat suitability, but this is unlikely to be of much help in elucidating pattern as all four species have quite generalized habitat preferences and various of them are sympatric somewhere in the area, so their broad-scale habitats are relatively similar, or, at least overlap broadly. Molecular studies (Smith et al. 2005) showed that Ruamahanga and southern Wairarapa populations of upland bully are closely similar, supporting the likelihood that they have recent, shared ancestry and possible spread there from the northern South Island, but further study is needed. This species looks to have spread up the eastern flanks of the mountain ranges of the southern North Island.

17.16 Bridging of Cook Strait

It has long been recognised that several strictly freshwater fish species, such as dwarf galaxias (see Fig. 12.2 – blue symbols), brown mudfish (see Fig. 14.3 – brown symbols), and upland bully (see Fig. 15.2 – blue symbols), are present on both sides of Cook Strait (McDowall 1970, 1990) and this is attributed to former land connections across the strait at several times in the past, most recently in the Pleistocene (Fleming 1979; Lewis and Carter 1994; Lewis et al. 1994). As noted above, populations of non-diadromous species from the small peninsula of land that connected the southern North Island to the South Island (see Fig 3.3) may

have been the source of North Island populations, or there could have been more widespread dispersal from North and South Island rivers that became confluent between the two islands at times when Cook Strait was widely bridged in Pleistocene times.

17.17 Non-diadromous Fish Species on D’Urville Island

Most near-shore islands around New Zealand have no non-diadromous fishes, but D’Urville Island is an exception, with its populations of dwarf galaxias (see Fig. 12.2, arrow 4). This is consistent with this species’ presence in nearby Marlborough Sounds streams. Upland bully is, however, absent from both D’Urville Island and streams of the Marlborough Sounds, which might be regarded as an interesting contrast, given the apparently broad habitat tolerances and vigorous reproductive habits of upland bully (McDowall 1990; McDowall and Eldon 1997); it seems like a generally successful invader.

17.18 Impoverished Fish Faunas of Kahurangi National Park and Northwest Nelson in the Northern South Island

Non-diadromous fish species are rare in the northwestern South Island, with dwarf galaxias generally absent from Golden Bay catchments (see Fig. 12.2, arrow 6 – blue symbols), upland bully present, though only rarely (see Fig. 15.2, arrow 5 – blue symbols), and there are only occasional populations of brown mudfish on the west coast of the northern South Island (Mangarakau Swamp – see Fig. 14.3, arrow 6 – brown symbols). None of these species has been found in Kahurangi National Park a little further to the south (Jowett et al. 1998). Reasons for these patterns are unclear, though Jowett et al. (1998) attributed general absence of non-diadromous species from streams of Kahurangi National Park to “biogeographic isolation of westward draining rivers dating from the period when the mountains were formed, rather than to glaciation”, though they discussed no detail. Once more (as in western Taranaki – see Section 17.11), the occasional presence of brown mudfish conflicts with the general pattern of absence of other non-diadromous species (see Fig. 14.3, arrow 4).

17.19 Implications of Pleistocene Glaciation in the West Coast of the South Island

Patterns of fish distributions in Westland (where *Nothofagus* beech forest associations are absent from the areas that were most heavily affected by glacial advances and seasonally permanent ice sheets – Willett 1950; Wardle 1963) also exhibit an

absence of non-diadromous freshwater fishes – first identified by Main (1989). Three non-diadromous fish lineages appear to have been affected: brown mudfish is widely present, extending south to about Okarito (see Fig. 14.3, arrow 8 – brown symbols), whereas dwarf galaxias (see Fig. 12.2, arrow 9 – blue symbols) and upland bullies (see Fig. 15.2, arrow 8 – blue symbols) both extend south only as far as the Hokitika River. Different southern boundaries of these species may reflect their differing capacities to spread southwards after glacial retreat or, alternatively, they may reflect lesser impacts of glaciation on wetland habitats where mudfish live, in contrast to the stream habitats suited to, and inhabited by, dwarf galaxias or upland bully (or perhaps both processes may have been implicated). A third possible explanation may be that dwarf galaxias and upland bully have arrived in the West Coast area more recently than brown mudfish, and so have had less time to spread south than the mudfish has – molecular evidence might be informative. The distribution of brown mudfish is centred at much lower elevations than dwarf galaxias and upland bully, and the various habitats occupied by these species may have been differentially influenced by glaciation, though the detail is unclear.

There does seem a somewhat consistent and distinctive ability of mudfish (and also koura – see McDowall 2005) to persist in the face of major habitat perturbations. Alternatively, brown mudfish (and also koura) may have been redistributed southwards, as far as Okarito, after the perturbation of habitats caused by glaciation had been repaired (see Section 14.4 and Fig. 14.3, arrow 8 – brown symbols), in a way that other the fish species were unable to (as also to the west of the recently volcanically active Mt Taranaki – compare presence of brown mudfish west of Mt Taranaki (see Fig. 14.3, arrow 4, Fig. 15.6 – brown symbols; Fig. 15.6), with the absence there of upland and Cran's bullies (see Fig. 15.2, arrow 3, Fig. 15.6, and Fig. 17.2: see Section 17.11 of this chapter, also). The fact that both dwarf galaxias and upland bully extend south only as far as the Hokitika River may, however, not be coincidental, but may result from parallel or comparable dispersal events and processes. The southern boundaries of dwarf galaxias and upland bully exhibit interestingly close concordance with Soons' (1992) observation that the northern limits of major West Coast Pleistocene ice advance were south of the village of Ross, just a few kilometres south of the Hokitika River. I refer elsewhere to Wallis and Trewick's (2009: 3563) suggestion that some freshwater fish lineages were "expunged" from western drainages by Pleistocene glaciation.

It is interesting that though there are clear impacts from glaciation on western slopes of the Southern Alps (the 'beech gap'), there are no comparable impacts on the eastern slopes – no freshwater fish distribution pattern gives any hint of effects of glaciation comparable to that on the west. This could have multiple explanations: glaciation did not extend downstream to sea coasts on the east, so that there remained broad alluvial plains and river systems downstream from the emergent glaciers. Also, it seems clear that there has been dispersal of freshwater fish lineages in a north-south direction across the broad Canterbury Plains to the east, probably as a result of the rivers draining the eastern slopes of the Southern Alps wandering laterally across the plains, making varied catchment connections and

facilitating freshwater fish dispersal. Many freshwater fishes have broad latitudinal ranges across the plains: Canterbury galaxias, alpine galaxias, Canterbury mudfish and upland bully.

17.20 Geological History and the Biogeography of Fish Species Near the Lewis Pass

Discussion in a previous section explored a series of biogeographic disjunctions in the vicinity of the Lewis Pass in the northern/central South Island. These summarise as follows:

- (i) There are populations of northern flathead galaxias in tributaries of the upper reaches of the western flowing Rappahannock and Maruia Rivers (arrow 4) – both Buller River system. This lineage is found also in upper reaches of the Motueka River (see Fig. 11.2 – red symbols, arrow 1), and is widely present in northeastern and eastern drainages, such as the Wairau, Awatere and Clarence Rivers (see Fig. 11.2, arrow 15 – red symbols; Fig. 17.6, arrows 8 and 9).
- (ii) In close proximity, somewhat to the southeast of the above, are the northernmost populations of Canterbury galaxias, in the east-flowing Lewis River (see Fig. 17.6, arrow 6), and this species occurs widely to the south in rivers of the intermontane valleys of inland Canterbury (see Fig. 11.2 – red symbols, Fig. 17.6; McDowall 1970, 1990).
- (iii) There is (or at least there formerly was, as no specimens have been collected recently despite efforts to do so) a population of upland longjaw galaxias near the Lewis Pass in upper tributaries of the west-flowing Maruia River near the Lewis Pass (see 12.4, arrow 1), but this species is not otherwise presently known from the Waiau which drains east from the Lewis Pass, but only in quite disjunct eastern and more southern catchments (Hurunui, some 50 km away, and then in the Rakaia, and other rivers further south – see Fig. 12.4 – black symbols).
- (iv) A further apparent lineage split involves dwarf galaxias, once more present in these same west-flowing Maruia tributaries (see Fig. 12.2, arrow 16 – blue symbols) and more widely, whereas a probable sister taxon, the alpine galaxias, is found in streams draining the eastern side of the Lewis Pass (12.2 – green symbols); both species are also found widely in a zone of sympatry to the northeast in upper tributaries of certainly the Wairau and Clarence. Waters et al. (2006) confirmed site sympatry of dwarf galaxias and alpine galaxias in two Wairau River tributaries, from molecular data, but there is a need for clarification of other identifications/locations of fish in this area. BurrIDGE et al. (2007) also showed that Pelorus/Wairau stocks of dwarf galaxias form a sister clade of populations in the Motueka River further to the west, all of these being a sister clade to North Island populations (as represented by samples from the Manawatu and Hutt Rivers), and then all of these to populations

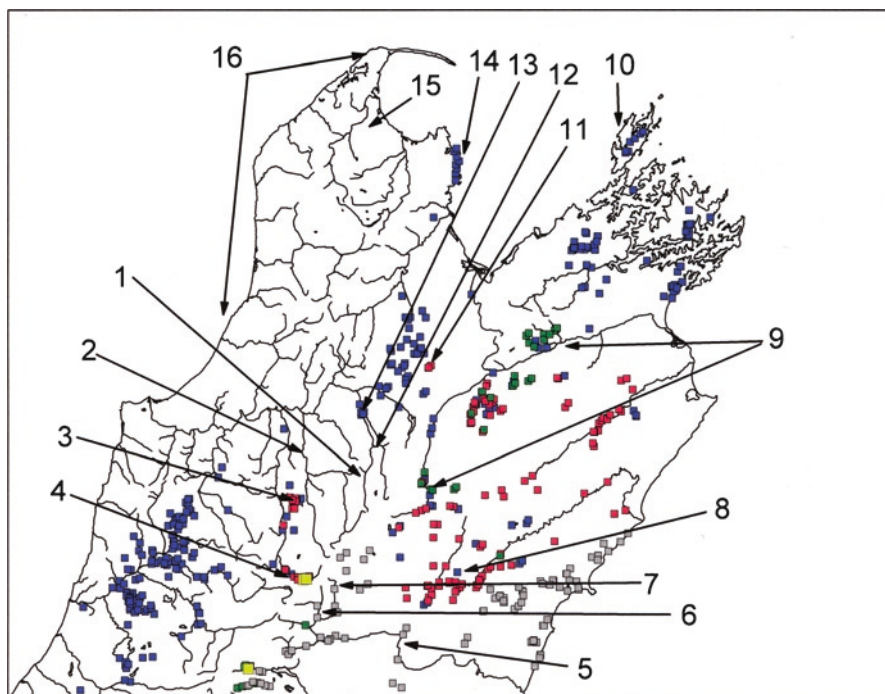


Fig. 17.6 Distributions in the northern South Island of: *Galaxias* 'northern' (■); Canterbury galaxias *Gl. vulgaris* (■); dwarf galaxias, *Gl. divergens* (■); alpine galaxias, *Gl. paucispondylus* (■); and upland longjaw galaxias, *Gl. prognathus* (■). **Arrows** - ↑1 – Matakitaki River; ↑2: Glenroy River; ↑3: Rappahannock River; ↑4. Maruia River; ↑5. Waiaru River; ↑6. Lewis River; ↑7 Boyle River; ↑8: Clarence River; ↑9: Wairau River; ↑10: D'Urville Island; ↑11: Motueka River; ↑12: Sabine and D'Urville Rivers; ↑14: Abel Tasman National Park streams; ↑15: Absence from Golden Bay; ↑16: Absence from northern West Coast and Kahurangi National Park streams

from the Buller River and then further to the southwest in the West Coast (Taramakau and Hokitika Rivers). Determining the place of D'Urville Island dwarf galaxias populations, in relation to all of these populations would be interesting.

- (v) And in addition, upland bully is widespread across much of the northern South Island, but again the genetics of populations in the vicinity of the Lewis Pass are unstudied.

Thus there is a series of highly idiosyncratic, sometimes discordant, distributions among several non-diadromous species or species groups, in an area that can have had only a single geological/geomorphological history. These various lineages may have occupied the area for different lengths of time, or perhaps different species groups have responded to these geological events in individualistic ways.

The place in fish lineage histories of a headwater capture of the east-flowing Lewis River headwaters by the Maruia River, suggested long ago as a possible

explanation of some of these fish species' distributions (McDowall 1970), and the headwater capture itself, as hypothesised by Soons (1992) from a purely geomorphological perspective, is thus highly uncertain, or at least inconsistent across the different fish clades. Further study is needed of distribution patterns in this area, and of particular interest would be molecular data on the stocks of upland bully, which is widespread there.

A very deep separation of upland bully stocks, discussed by Smith et al. (2005), involves:

- (i) One group of populations that is present in the eastern South Island, from North Canterbury (Clarence and Conway Rivers) southwards to the Mackenzie Basin (see Fig. 15.4) and the Waitaki River, and found also in coastal drainages of the Kakanui River south to the Waikouaiti.
- (ii) A second group that is present in Central Otago in the Clutha River catchment, and across Southland.

Note, however, that whereas the Clarence River stocks of northern flathead galaxias relate to populations further north in the Awatere and Wairau, the upland bully populations in these areas exhibit an ancestry closest to populations further to the south. Here, yet again, we have an instance of individualistic, divergent population relationships in different groups of lineages across the same landscape.

This pattern closely resembles a somewhat simplified pattern seen in the *Galaxias vulgaris* species complex (discussed in Section 11.2.1, above).

17.21 Differing Patterns of Distribution and Speciation Across the Eastern South Island

Further patterns in the distributions of non-diadromous fishes of the eastern flanks of the South Island mountains, primarily in the Southern Alps, from Marlborough to Stewart Island, differ very deeply across groups. Upland bully is simplest, being present very widely across this entire area (see Fig. 15.2 – blue symbols), though there may be unrecognised taxonomic diversity there (Smith et al. 2005; Stevens and Hicks 2009). However, if there is, that diversity is probably not comparable with the taxonomic diversity in the *Gl. vulgaris* species complex across the same area. This pattern is distinctly different, again, from that in the five recognised pencil-galaxias species that are together present very widely across this same area (see Fig. 12.2–12.4), but exhibit individualistic differences in patterns, with diversification significantly in the Mackenzie Basin (upper Waitaki River), where four of them are found (see Fig. 12.3). There is nothing comparable to this in either the *Gl. vulgaris* species complex (see Chapter 11) or upland bully (Section 15.3). Moreover, there are ten species/lineages of the *Gl. vulgaris* species complex across the same area, but they have done their diversification mostly in Central Otago and somewhat further to the south in Southland and Stewart Island (see Figs. 11.2,

11.3). And so, again, deeply different processes of dispersion and speciation characterise the histories of upland bully and each of the various galaxiid complexes. And it is not as if the eleotrid bullies have arrived in the area recently, as fossils are known from the Miocene of Central Otago (McDowall et al. 2006b), though phylogenetic connections of the fossils to extant taxa are unknown, and this will not be easily elucidated.

Canterbury mudfish is different again, in being a Canterbury endemic found in waterways (often wetlands) entirely out on the plains, and in having its affinities with a rather more diverse species complex further to the north (see Chapter 14).

17.22 Affinities of Populations Along the Coastal Strip South of the Mouth of the Waitaki River

There is, however, some interesting commonality in patterns of distribution and relationship of non-diadromous species in the rivers draining several small, mountain ranges near the east coast of the South Island to the south of the Waitaki River (see Fig. 11.2, arrows 12 and 13). Molecular studies of members of the *Gl. vulgaris* species group in the Kakanui River show that at least some of the populations there belong to Canterbury galaxias present primarily to the north, and so are different from populations a little further inland (west), in the Taieri River, and also from those further to the south and west into Otago. Somewhat in parallel, molecular studies of upland bully populations in the eastern South Island also show that populations in rivers south as far as the Waikouaiti River, are similarly closest to upland bully populations in Canterbury, to the north, rather than to populations further to the west and south in the eastern South Island (Smith et al. 2005).

Thus in both groups, there appears to have been some spread south into these small coastal mountain ranges and the rivers that drain them from Canterbury to the north in a parallel way, though upland bully has spread further south than Canterbury galaxias. This is perhaps not surprising, given the much wider environmental tolerances of upland bully, compared with the galaxiid. None of the ‘pencil galaxias’ group is present in these coastal rivers, apart from the isolates of lowland longjaw galaxias in the Kakanui/Kauru River catchment (see Section 12.5).

Spread south along this coastal strip may have been assisted by shifting connections made among these small river systems when sea levels were significantly lowered during the Pleistocene (Kirk 1994; Craw and Norris 2003).

17.23 Diversification in the Mackenzie Basin

The modest diversification of four species in the pencil-galaxias species group in the Mackenzie Basin (see Figs. 12.2–12.4) is highly distinctive – there is nothing comparable in the *Galaxias vulgaris* species complex, nor in upland bully. Diversity in pencil galaxias in the Mackenzie Basin could perhaps be attributed to the fact that riverine habitats across the basin were not as extensively obliterated by glacial

advance in the way the intermontane valleys of the Canterbury rivers were, and so habitats might have remained available to them there through the Pleistocene (Fitzharris et al. 1992). However, unlike the pencil-galaxias, both Canterbury galaxias and upland bully are widespread through the same Mackenzie Basin riverine habitats, with no known hint of diversification or speciation there (Waters and Wallis 2001a, b; Smith et al. 2005).

17.24 Endemism in the Central South Island

Given the above patterns, there is no evidence for reduced overall endemism in the freshwater fish fauna in the central/eastern South Island. As just discussed, the Mackenzie Basin is actually an area of somewhat higher species richness and endemism – bignose galaxias (see Figs. 12.2, 12.3 – red symbols) and lowland longjaw galaxias (see Figs. 12.3, 12.4 – yellow symbols) are local near endemics, while alpine galaxias (see Figs. 12.2, 12.3 – green symbols) and upland longjaw galaxias (see Figs. 12.3, 12.4 – black symbols), as well as Canterbury galaxias (see Fig. 11.2 – red symbols) and upland bully (see – Fig. 15.2 blue symbols) also being present there.

17.25 Non-diadromous Fish Species and the Glacial Lakes of the Eastern Southern Alps

Non-diadromous galaxiids are not usually found upstream of major, sub-montane, glacial lakes – none are known from above any of the Waimakariri or Rakaia River lakes, nor in the headwaters above the Waiau (Southland) lakes, i.e. Lakes Te Anau and Manapouri, as in the Eglinton River. However, there are some interesting exceptions:

- (i) Dwarf galaxias is present in a single tributary of Lake Rotorua in the Nelson Lakes.
- (ii) Upland longjaw and Canterbury galaxias both occur in tributaries of the Hurunui River upstream of Lake Sumner.
- (iii) Several non-migratory species are found upstream of the three major Waitaki Valley lakes (Tekapo, Pukaki and Ohau), e.g. Canterbury galaxias, alpine galaxias, upland longjaw galaxias (see Fig. 12.3, arrow 1) and upland bully are present upstream of Lake Tekapo, Canterbury galaxias, upland longjaw and upland bully upstream of Lake Pukaki, and Canterbury galaxias, upland longjaw galaxias and upland bully upstream of Lake Ohau (see Figs. 11.2, 12.3).
- (iv) Alpine galaxias is in the Lochy River (Lake Wakatipu), and this presumably points to the known fact that southern arm of Lake Wakatipu once, or perhaps on several former occasions, drained south into the Mataura River, as discussed above, at which time there may have been a river where southern arm of the lake now lies (see Fig. 12.2, arrow 11).

How did they get into these river systems upstream of the existing lakes? Given the various *Galaxias* species' known preferences for coarse, cobble/boulder-substrate, swiftly-flowing, riffly streams (Bonnett 1990, 1992; McDowall 1990), it seems unlikely that they have invaded the rivers upstream of these lakes by moving through the stationary waters of the sandy-bedded lakes themselves – though this might seem more credible for upland bully, which may be found around the shores of inland lakes and is present in the small tributaries around Lakes Tekapo and Ohau. How these galaxiids were able to occupy streams above these big glacial lakes is a question of some interest, given their habitat preferences. It is especially difficult to imagine a fish like an upland longjaw galaxias swimming 20–30 km around the shores of big lakes like Tekapo, Pukaki, and Ohau, but it is present upstream of all three. Is it possible that streams once flowed down the glacial valleys, parallel, and probably marginal, to the glacial moraines, when these were still extensively frozen, perhaps fed by lateral melt of the moraines? Some interesting observations of the behavior of glaciers in the Sierra Nevada of California, by noted pioneering nineteenth century conservationist John Muir might bear on this scenario. Muir told of small streams flowing across the surfaces of glaciers, through the layers of gravel on the retreating glacial ice and moraines (Muir 2004), and the same could have been true of the glaciers of the Mackenzie Basin. If so, these species could have been already present upstream of the lakes prior to the final melting of the moraine and the formation and filling of the lakes themselves?

- (i) As detailed earlier, there are populations of both the roundhead morph (*Gl. gollumoides*) and flathead morph (Southland flathead galaxias) of the *Gl. vulgaris* complex in the Von River, which now drains north into the southern shores of Lake Wakatipu, and this no doubt reflects the fact that the Von previously flowed south into the upper reaches of the Oreti River (Burridge et al. 2006) (see Fig. 11.2, arrow 6, Fig. 11.3, arrow 4); however, again, no upland bully are found there, despite this species being widespread across Southland, and it perhaps did not reach Southland until after the Von was captured; or maybe the species was once present but was extirpated in the Von.
- (ii) Alpine galaxias, southern roundheads and upland bullies are all present in the Mararoa River, upstream of the Mavora Lakes – Mararoa River, in the Waiau River system, and they may reflect vestiges of old distributions affected by glaciation – the Mavora Lakes are very long and slender drowned valleys.
- (iii) There is also a single record of upland bully in a tributary of Lake Te Anau, in Southland and this identification needs to be checked.

17.26 Freshwater Fish Populations of the Intermontane Valleys of the Eastern South Island

The large intermontane valleys of the eastern slopes of the Southern Alps and their foothills (especially the Waimakariri, Rakaia, Rangitata and Waitaki Rivers) were profoundly affected by New Zealand's long series of alternating Pleistocene

glacial/inter-glacial events – various of the valleys filled, probably several times, with ice that was sometimes hundreds of metres or more thick and which at times spilled out of the valleys onto the upper Canterbury Plains. The last of these glacial advances seems likely to have left the strongest biological imprint as it will have been imposed upon previous impacts, or have overwritten them, both temporally and spatially (Willett 1950; Gage 1958; Soons 1992). A biogeographical implication of these events is that the fish species that are now found in these intermontane valleys must have penetrated them when rivers eventually replaced the glaciers following the last glacial retreat. This applies particularly widely to the populations of Canterbury galaxias and, as well to each of the relevant South Island species in the pencil-galaxias species group (alpine, bignose, lowland and upland longjaw galaxias); perhaps also some southern populations of dwarf galaxias were affected, and also upland bully.

The very broad distribution of alpine galaxias brings this species into close proximity to, or sympatry with:

- (i) Northern flathead galaxias and upland bully in the upper reaches of the Wairau and Clarence Rivers
- (ii) Canterbury galaxias, upland longjaw galaxias and upland bully in the eastern Canterbury Southern Alps
- (iii) Southland flathead galaxias and Gollum galaxias, and upland bully in the upper Waiau–Mavora Lakes, as mentioned above

Whatever the details of various areas of sympatry, it is clear that the processes of dispersal and diversification that have generated the very broad distribution patterns in the intermontane valleys, in the widespread alpine galaxias and upland bully have been very different from the processes of speciation and dispersal applying to various multiple, more localised lineages in the *Galaxias vulgaris* species complex that are variously sympatric with alpine galaxias and upland bully.

17.27 Absence of Non-migratory Fish Species in Fiordland, West of the Waiau River in Southland

None of the southern non-migratory fish species, of *Galaxias* or *Gobiomorphus*, is found in rivers and lakes west of the Waiau River in Southland. The Waiau River catchment arises in the Clinton River at the head of Lake Te Anau and also in Lakes Fergus and Gunn in the upper reaches of the Eglinton River, again at the head of Lake Te Anau, in Fiordland. These rivers all drain southwards into Lake Te Anau, then further south again via the Waiau River, to, and through, Lake Manapouri, and from there to sea in western Foveaux Strait (the area to the east of the dotted line in Fig. 10.4). Non-migratory *Galaxias* species are present widely in the lower reaches of the Waiau, in tributaries both to the east and west of the river's mainstem

(see Fig. 11.2, arrow 7; Fig. 11.3, arrow 5), but none is known to spread further west, for example, into separate catchments involving Lake Hauroko and the Wairaurahiri River (McDowall and Sykes 1996), which drains south to Foveaux Strait, or in other rivers further to the west, again, into southern Fiordland. Upland bully is similarly widespread across the Southland Plains as far west as the Waiau River catchment, but also spreads no further west (see Fig. 15.2).

17.28 Fish Fauna of Banks Peninsula, and Those of the Canterbury Plains

The fish faunas, especially of the rivers of the Canterbury Plains, are distinct from that of Banks Peninsula, which lies at the eastern fringe of the plains. The unstable, shingly, braided rivers of the plains and coastal regions (see Fig. 10.3) now have fish communities that are dominated mostly by diadromous species such as common smelt, in some rivers by Stokell's smelt, and inanga, at low elevations, as well as common bully, bluegill bully, torrentfish, shortfin and longfin eels across much greater elevations and distances inland from the sea, and also non-diadromous species such as Canterbury galaxias, alpine galaxias and upland bully. On Banks Peninsula, however, there are very different habitats in steep, stable, boulder/cobble streams, sometimes in native forest, and a quite different array of species is found in these peninsula streams, particularly koaro, banded kokopu, and also torrentfish, bluegill bully, and occasional redfin bully. This is probably in part a question of instream habitat suitability (small streams with stable, coarse cobble/boulder substrates) and probably also that many of them have forested, or part forested catchments (which is likely to be of particular importance for koaro and banded kokopu) (McDowall 1990; Rowe et al. 1999). Thus, as is generally true of diadromous species across the whole of New Zealand, species composition is substantially an issue of availability of suitable habitats. Where there are suitable, accessible, habitats they will be present, with species composition relating to habitat suitability. Upland bully are interestingly sparse in Banks Peninsula streams; being non-diadromous, this species will have had difficulty colonising isolated small stream catchments, or recolonising them if extirpated, and it is likely that the small stream catchments on the peninsula are ephemeral enough to lead at times to local extirpation of upland bully (McDowall 1995).

17.29 History and Biogeography of the Nevis and Von Rivers, Clutha River System

Though the Southland roundhead species Gollum galaxias is present in the Nevis and Von Rivers and southern flathead also in the Von, in the Clutha River catchment (see Fig. 11.2, arrows 5 and 6), neither alpine galaxias nor upland bully are

present in these rivers, though are variously present across the Southland Plains, especially upland bully (see Fig. 15.2, arrow 11; Fig. 15.7) (see Waters et al. 2001). It is presently not in the streams that were captured, although absences of upland bully may be because it has been unable to cope with low temperatures during periods of glacial advance – upland bullies may be intolerant of very cold temperatures, or perhaps they were never present in either river prior to their capture by parts of the Kawarau/Clutha system. Here, again, are examples of a lack of congruence between faunal elements that commonly co-occur elsewhere across a common landscape history. Alternatively, it is possible that upland bully arrived in this area more recently than the two galaxiids. Absence of alpine galaxias from the Von is unlikely to be so easily explained.

17.30 Impoverished Fish Fauna of the Kawarau River, Clutha River System

The Kawarau River has its source in Lake Wakatipu to the west, and it flows eastwards to join the mid-Clutha River at Cromwell. Non-diadromous fish species are generally absent from the Kawarau, with several distinctive, localised exceptions, such as:

- (i) The presence of Gollum galaxias in the Nevis River (see Fig. 11.2, arrow 5), as detailed earlier (see Section 17.29, above)
- (ii) Clutha flathead galaxias in the Bannock Burn close to the Kawarau/Clutha confluence (see Section 11.25 and Fig. 11.3, arrow 3)
- (iii) Alpine galaxias in the Lochy (see Fig. 12.2, arrow 12, Section 11.27 and Section 17.25)
- (iv) Southern flathead galaxias and Gollum galaxias in the Von River (see Fig. 11.2, arrow 6; Fig. 11.3, arrow 4) as detailed earlier, these being vestiges of former, distinctive, southern, fluvial connections to the Mataura and Oreti Rivers of inland Southland

By contrast with this absence from the Kawarau River, there are both upland bully and various of the *Gl. vulgaris* complex lineages in the other main branch of the upper Clutha, and particularly in its major inland tributaries, the Lindis and Manuherikia Rivers (see Fig. 11.2, arrow 3; Fig. 11.3, arrow 1; Fig. 15.7, arrows 1 and 2). The otherwise general absence of non-diadromous native fish from the Kawarau catchment is thus striking.

During the Pleistocene there were extensive glaciers in what is now Lake Wakatipu, and at some stages of climatic warming and glacial retreat, discharge from what are now some of the Lake Wakatipu sub-catchments, flowed south via the south arm of Lake Wakatipu, or its precursor, into the upper Mataura River, perhaps as recently as 5,000 years ago (Lowe and Green 1992; Craw and Norris 2003). This old fluvial connection probably explains how there came to be a population of alpine galaxias in the Lochy River, which now discharges into the south arm of Lake Wakatipu (see Fig. 12.2, arrow 13 – green symbols), but this species is present

nowhere else in the Clutha, except for the uppermost tributaries of the Manuherikia, another rather distant Clutha tributary (see [Section 12.2](#)). As climate warmed, deposition of glacial moraine at the southern end of the present south arm of Lake Wakatipu created a low gravelly divide that prevented the lake from continuing to discharge southwards into the Mataura. An alternative outlet from Lake Wakatipu then developed as the present east-flowing Kawarau River (Lowe and Green [1992](#)). Possibly, the general absence of non-migratory galaxiids from the Kawarau relates to this Pleistocene history; they have not invaded up the Kawarau from the Clutha, since the Clutha connection became established. Presence of *Galaxias* ‘species D’ in the Bannock Burn is a likely reflection of a connection of this stream to the main-stem Clutha that pre-dates the drainage of Lake Wakatipu west via the Kawarau.

17.31 History and Biogeography of the Cardrona River

Changing fluvial connections of the Cardrona River were discussed above (and see [Craw and Norris 2003](#)). Given the fact that the Cardrona once flowed south into the Kawarau, and that the Kawarau seems to carry virtually no non-migratory species (as just discussed in the previous paragraph), it might have been expected that the Cardrona would also have none, but it does have populations of Clutha flathead galaxias, a lineage that is widespread across the Clutha. Presumably, after flow reversal in the Cardrona River ([Craw and Norris 2003](#)), this galaxiid entered the Cardrona from the upper Clutha and its tributaries (see [Fig. 11.3](#), arrow 2), and is now widespread there. A single recently-sampled site revealed upland bully there (of 17 sites sampled in the river), as if it is just ‘hanging on’ in the Cardrona. Maybe it has only recently reached the Cardrona – perhaps both are true.

17.32 Bridging of Foveaux Strait

There was a land connection across Foveaux Strait between South Island and Stewart Island during the Pleistocene ([Fleming 1979](#)), and so the presence on Stewart Island of Gollum galaxias, southern flathead galaxias, and upland bully (see [Fig. 11.2](#), arrow 9; [Fig. 11.3](#), arrow 7; [Fig. 15.2](#), arrow 10) is unsurprising, since all three species are widely present across the Southland Plains to the north of Foveaux Strait. Alpine galaxias has not joined these species on Stewart Island, as far as is known.

17.33 Recruitment Issues in the Southern South Island

Site species richness of diadromous species in rivers flowing into Foveaux Strait is comparatively low. Diadromous species like banded kokopu, koaro, torrentfish, bluegill and giant bullies are at best sparse and sporadic in these rivers ([McDowall 1994](#); [McDowall and Lambert 1996](#); [McDowall and Sykes 1996](#); and see [Fig. 10.2](#)). This

applies to most freshwater fish families, and may relate to recruitment problems for diadromous species associated with strong oceanic currents that sweep from the west through Foveaux Strait (Carter 2001). Chiswell et al. (2003) postulated that juvenile recruitment into the populations of the marine rock lobster, *Jasus edwardsii* (Crustacea), in the seas along the Fiordland and south Westland coastlines of the South Island, may actually derive from populations in Tasmania, ca. 2,000 km west across the Tasman Sea (Ovenden et al. 1992), thus implying that they consider that there could be local self-recruitment problems for rock lobsters in Fiordland. The diadromous fish of the area may also have similar recruitment problems for similar reasons (though there is no possible comparable source for most of them in Tasmania). Moreover, there are productive whitebait fisheries in the southern rivers of the West Coast and in Southland (McDowall 1984), and eels successfully recruit to them. Much remains to be learned about the population- and recruitment-ecology of these diadromous fish species, and the questions raised here are unlikely to be easily or rapidly resolved.

17.34 Freshwater Fishes at the Chatham Islands

In the light of those diadromous species that are present at the Chathams (Skrzynski 1967; Rutledge 1992, and see Table 9.2), there are some perhaps surprising absences there, such as shortjaw kokopu, common bully, bluegill bully, and torrentfish. The effects of ocean currents, and the recruitment of juveniles into river systems from the sea, may be a critical determinant of the freshwater fish fauna of the Chatham Islands. Recruitment from the sea back to these highly isolated islands may be a problem for all diadromous species, and the mechanisms that enable diadromous species to recruit to Chatham Island streams are unknown.

It is not known whether the diadromous freshwater fish populations of the island:

- (i) Self-recruit
- (ii) Derive their recruits from mainland New Zealand
- (iii) Perhaps some of both

Given the low likelihood of regular, cohort-scale, dispersal of diadromous freshwater fish progeny from New Zealand to the Chathams (discussed earlier – Section 9.6), recruitment there may need to be addressed as occasional arrivals (historical processes), rather than regular recruitment or dispersal (ecological processes). Nothing is known. Some of the diadromous species absent from the Chathams are those also lacking or sparse in western Fiordland, southern Southland and Stewart Island, so it is possible that some species are more robust migrants than others. Or, recruitment may simply be a stochastic process affected by the number of larvae being spread around the coastal seas of New Zealand, i.e., the more larvae of a diadromous species there are at sea, the greater is the likelihood that some will expatriate to the Chatham Islands, but if that is an explanation, it needs to be recognised that the torrentfish is greatly abundant in rivers along the east coast of the South Island but is absent from the Chathams. Possibly, Chatham Island populations

of some diadromous fish species need to be viewed as ecological sinks (Pulliam 1988). A distinctive feature of the Chathams freshwater fish fauna is the presence of common smelt, a species that is recorded from no other minor islands in the New Zealand area. Populations could be maintained at the Chathams in the medium-term by coastal dispersal of fish derived from landlocked populations in the Te Whanga Lagoon, a large, low-elevation brackish lake on Chatham Island, where common smelt is very abundant, and which occasionally opens to the sea. Most records of common smelt from the Chatham Islands are either in tributaries of the Te Whanga Lagoon, or are present as populations in small, landlocked lakes. No non-diadromous species other than the Chatham mudfish is known from these islands, nor, other than the smelts, are entirely lacustrine populations of diadromous species reported from there, though this question has not been addressed.

17.35 Freshwater Fishes on the Auckland and Campbell Islands

These two small island groups, several hundred kilometres south of Stewart Island, have koaro in their streams, constituting the most southerly range of any western Pacific galaxiid. Whether these fish recruited originally from Tasmania to the north-west, or from New Zealand more to the north-east is unknown and would form an interesting question for molecular analysis (preliminary studies suggest derivation from New Zealand – again assuming that there is self-recruitment to these islands at the cohort scale). These islands are not of Gondwanan age, but are volcanic, and are thought to have emerged late in the Cenozoic (Campbell and Hutching 2007). The presence of koaro in the streams on these islands is therefore clearly not an outcome of former land connections. These islands may actually never have had any land connection to mainland New Zealand, being regarded as basalt volcanoes, Campbell Island is c. 11–6 million years old and the Auckland Islands 19–12 million years old (Campbell and Hutching 2007), and so they are greatly post-Gondwanan and their biotas are derived by dispersal processes. Michaux and Leschen (2005) argued that Campbell Island must have remained above water “to account for the persistence of palaeo-endemics”, the so-called remnants of an original Gondwanan flora and fauna, but geological evidence is inconsistent with that view. Regardless, the diadromous koaro does not belong among them, but probably dispersed there.

References

- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Anon (n.d.) The year of the lahar, 2007: natural hazards 2007. NIWA/GNS, Wellington, N Z
- Ballance PF, Williams PW (1992) The geomorphology of Auckland and Northland. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 210–232

- Barker JR, Lambert DM (1988) A genetic analysis of populations of *Galaxias maculatus* from the Bay of Plenty: implications for natal river return. *N Z J Mar Freshwater Res* 22:321–326
- Berra TM (2007) Freshwater fish distribution. University of Chicago, Chicago, 606 pp
- Bonnett ML (1990) Age and growth of alpine galaxias (*Galaxias paucispondylus* Stokell) and longjawed galaxias (*G. prognathus* Stokell) in the Rangitata River, New Zealand. *N Z J Mar Freshwater Res* 24:151–158
- Bonnett ML (1992) Spawning in sympatric alpine galaxias (*Galaxias paucispondylus* Stokell) and longjawed galaxias (*G. prognathus* Stokell) in a South Island, New Zealand high-country stream. *N Z Nat Sci* 19:27–30
- Bowen FE (1964) Sheet 15 – Buller. Geological map of New Zealand 1:250,000. Department of Scientific and Industrial Research, Wellington, N Z
- Boyer SL, Giribet G (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones; Cyphophthalmi). *J Biogeogr* 36:1084–1099
- Boyer SL, Clouse RM, Benavides LR, Sharma P, Schwendinger PJ, Karunarathna I, Giribet G (2007) Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *J Biogeogr* 34:2076–2085
- Bradshaw M, Soons J (2008) The lie of the land. In: Winterbourn MJ, Knox GA, Burrows C, Marsden I (eds) *The natural history of Canterbury*. Canterbury University Press, Christchurch, N Z, pp 15–36
- Brook FJ (1999) Stratigraphy and landsnail faunas of Late Holocene coastal dunes, Tokerau Beach, northern New Zealand. *J R Soc N Z* 29:337–359
- Burridge CP, Craw D, Waters JM (2006) River capture, range extension and cladogenesis: the genetic signature of vicariance. *Evolution* 60:1038–1049
- Burridge CP, Craw D, Waters JM (2007) An empirical test of freshwater vicariance via river capture. *Mol Ecol* 16:1883–1895
- Burrows CJ, Wilson HD (2008) Vegetation of the mountains. In: Winterbourn MJ, Knox GA, Burrows CJ, Marsden I (eds) *The natural history of Canterbury*. Canterbury University Press, Christchurch, N Z, pp 279–346
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 236 pp
- Campbell HJ, Landis CA (2005) Exploring constraints on the antiquity of terrestrial life in New Zealand. *Geol Soc N Z Misc Publ* 119A:12
- Carter L (2001) Currents of change: the ocean flow in a changing world. *Water Atmos* 9(4):15–17
- Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Mol Phyl Evol* 52:470–487
- Chiswell SM, Wilkin J, Booth JD, Stanton B (2003) Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? *Mar Ecol Prog Ser* 247:173–182
- Clarkson BD (1990) A recent review of vegetation development following recent (<450 years) volcanic disturbance in North Island, New Zealand. *N Z J Ecol* 14:59–71
- Cole JW (1970) Structure and eruptive history of the Tarawera volcanic complex. *N Z J Geol Geophys* 13:879–902
- Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proc R Soc Lond B Biol Sci* 261:293–302
- Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. *Trends Ecol Evol* 8:429–433
- Craw D, Norris R (2003) Landforms. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, N Z, pp 17–34
- Craw D, Burridge CP, Upton P, Rowe DL, Waters JM (2008) Evolution of biological dispersal corridors through a tectonically active mountain range, New Zealand. *J Biogeogr* 35:1790–1802
- Daugherty CH, Gibbs GW, Hitchmough RA (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends Ecol Evol* 8:437–442
- Deely J, Sheppard D (1992) Heavy metals in the Whangaehu River: an example of a naturally contaminated river. Trace elements: roles, risks and remedies: Proceedings of the N Z Trace Elements Group Conf, Massey University, Palmerston North, N Z, pp 41–51

- Dijkstra LH, Jellyman DJ (1999) Is the subspecies classification of the freshwater eels *Anguilla australis australis* Richardson and *A. australis schmidtii* Phillipps still valid? *Mar Freshwater Res* 50:261–263
- Douglas BJ (1986) Lignite resources of Central Otago: Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessments and exploration models. *N Z Energy Res Devel Committee Publ* 104:1–368
- Edgar NB (2002) Sustainable catchment management: a role for volcanic eruptions? *Verhand Int Verein theor ang Limnol* 28:1167–1171
- Ericson GPG, Chistididis L, Cooper A, Irestedt M, Jackson J, Johansson S, Norman JA (2002) A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc R Soc Lond B Biol Sci* 269:234–241
- Eyles RJ, McConchie JA (1992) Wellington. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 382–406
- Fitzharris BB, Mansergh DG, Soons JM (1992) Basins and lowlands of the South Island. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 407–423
- Fleming CA (1979) *The geological history of New Zealand and its life*. Auckland University Press, Auckland, N Z, 141 pp
- Gage M (1958) Late Pleistocene glaciations of the Waimakariri valley, Canterbury, New Zealand. *N Z J Geol Geophys* 1:123–155
- Gibbs GW (2006) *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton, Nelson, N Z, 232 pp
- Gleeson DM, Howitt RLJ, Ling N (1999) Genetic variation, population structure and cryptic species within the black mudfish, *Neochanna diversus*, an endemic galaxiid from New Zealand. *Mol Ecol* 8:47–57
- Graf DL, O'Foighil D (2000) Molecular phylogenetic analysis of 28S rDNA supports a Gondwanan origin for Australasian Hyriidae (Mollusca: Bivalvia: Unionida). *Vie Milieu* 50:245–254
- Graf DL, Cummings KS (2007) Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionida). *J Moll Stud* 73:291–314
- Haas F (1969) Superfamily Unionacea Fleming 1828. In: Moore RC (ed) *Treatise of Invertebrate Paleontology, Part N Mollusca* 6, vol 1, Bivalvia. Geological Society of America/University of Kansas Press, Lawrence, KA, pp N411–N4114
- Heads M (1998) Biogeographical disjunction along the alpine fault, New Zealand. *Biol J Linn Soc* 63:161–176
- Heads M, Crow R (2004) The alpine fault biogeographic hypothesis revisited. *Cladistics* 20:184–190
- Healy J (1992) Central volcanic region. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 256–286
- Hopkins CL (1971) Production of fish in two small streams in the North Island of New Zealand. *N Z J Mar Freshwater Res* 5:280–290
- Jowett IG, Hayes JW, Deans N, Eldon GA (1998) Comparisons of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. *N Z J Mar Freshwater Res* 32:307–322
- Kamp PJJ (1992a) Tectonic architecture of New Zealand. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 1–30
- Kamp PJJ (1992b) Landforms of Hawke's Bay and their origin: a plate tectonic interpretation. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 344–366
- Kamp PJJ (1992c) Landforms of Wairarapa: a geological perspective. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 367–381
- Kennedy EM, Alloway BV (2004) Climate assessment, paleobotany and stratigraphy of a mid-Pleistocene lacustrine section, Ormond Valley, Gisborne. *N Z Ins Geol Nucl Sci Sci Rep* 2004(13):1–32

- Kennedy EM, Alloway BV, Mildenhall DC, Cochran U, Pillans B (2008) An integrated terrestrial palaeoenvironmental record from the mid-Pleistocene transition, eastern North Island, New Zealand. *Quat Internat* 178:146–166
- Kirk J (1994) The origin of Waihora/Lake Ellesmere. In: Davies J, Galloway L, Nutt AHC (eds) *Waihora/Lake Ellesmere: past present future*. Lincoln University/Daphne Brasell, Lincoln, N Z, pp 9–16
- Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA (2008) The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 143:173–197
- Lee D, Forsyth J (2008) Central rocks: a guide to the geology and landscapes of Central Otago. *Geol Soc N Z Guidebook* 14:1–84
- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust J Bot* 49:341–356
- Lee DE, McDowall RM, Lindqvist JK (2007) *Galaxias* fossils from Miocene lake deposits, Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *J R Soc N Z* 37:109–130
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) *Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea conference*, Christchurch, New Zealand, 27–30 November, 1992. Balkema, Rotterdam, The Netherlands, pp 119–137
- Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Mar Geol* 116:293–312
- Lowe DJ, Green JD (1987) Origins and development of the lakes. In: Viner A (ed) *Inland waters of New Zealand*. Department of Scientific and Industrial Research, Wellington, N Z, pp 1–64
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 107–143
- Main MR (1989) Distribution and post-glacial dispersal of freshwater fishes in South Westland, New Zealand. *J R Soc N Z* 19:161–169
- Mark AF, Adams NM (1973) *New Zealand alpine plants*. Reed, Wellington, N Z, 262 pp
- McAlpin J (1992) Glacial geology of the upper Wairau Valley, Marlborough, New Zealand. *N Z J Geol Geophys* 35:211–222
- McDowall RM (1964) The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara* 12:59–67
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1972) The species problem in freshwater fishes and the taxonomy of diadromous and landlocked populations of *Galaxias maculatus* (Jenyns). *J R Soc N Z* 2:325–367
- McDowall RM (1976) Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J R Soc N Z* 6:17–22
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1984) *The New Zealand whitebait book*. Reed, Wellington, N Z, 210 pp
- McDowall RM (1990) *New Zealand freshwater fishes: a natural history and guide*. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1994) Native fish populations of the Waiau River (Southland) and the impacts of the Lake Manapouri control structure (the Mararoa Weir). *NIWA Consult Rep SRCOO5:1–58*
- McDowall RM (1995) Understanding the absence of upland bullies from eastern Banks Peninsula. *Water Atmos* 3(4):17–19
- McDowall RM (1996) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 35:165–172

- McDowall RM (2005) Biogeography of the New Zealand freshwater crayfishes (Parastacidae, *Paranephrops* spp): restoration of a refugial survivor? *N Z J Zool* 32:55–77
- McDowall RM (2008) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM, Eldon GA (1997) Reproductive cycling and fecundity estimation in the upland bully. *J Fish Biol* 51:164–179
- McDowall RM, Lambert P (1996) Fish and fisheries values of the lower Maitai River: an assessment of values and implications of effluent discharges to the river. NIWA Consult Rep COO605/1:1–17
- McDowall RM, Lee DE (2005) Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *J R Soc N Z* 35:339–344
- McDowall RM, Pole M (1997) A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J R Soc N Z* 27:193–198
- McDowall RM, Sykes JRE (1996) Fish survey of the Wairaurahiri River, western Southland. NIWA Consult Rep SRC005/2:1–35
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. *N Z J Zool* 29:41–52
- McDowall RM, Waters JM (2003) A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. *J R Soc N Z* 33:675–691
- McDowall RM, Jellyman DJ, Dijkstra LC (1998) Arrival of an Australian anguillid eel in New Zealand: an example of transoceanic dispersal. *Environ Biol Fish* 51:1–6
- McDowall RM, Kennedy EM, Alloway BV (2006a) A fossil southern grayling, genus *Prototroctes*, from the Pleistocene of northeastern New Zealand (Teleostei: Retropinnidae). *J R Soc N Z* 36:27–36
- McDowall RM, Kennedy EM, Lindqvist JK, Lee DE, Alloway BV, Gregory MR (2006b) Probable *Gobiomorphus* fossils from the Miocene and Pleistocene of New Zealand (Teleostei: Eleotridae). *J R Soc N Z* 36:97–109
- Michaux B, Leschen RA (2005) East meets west: biogeology of the Campbell Plateau. *Biol J Linn Soc* 86:95–115
- Muir J (2004) The eight wilderness-discovery books. Diadem, London, 1005 pp
- Neall V (1992) Landforms of Taranaki and the Wanganui lowlands. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 287–307
- Oliver WRB (1928) The flora of the Waipaoa series (later Pliocene) of New Zealand. *Trans Proc N Z Inst* 59:287–303
- Ovenden JR, Brasher DJ, White RWG (1992) Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia. *Mar Biol* 112:319–326
- Pulliam HR (1988) Sources and sinks and population regulation. *Am Nat* 43:187–193
- Rowe DK, Chisnall BL, Dean T, Richardson J (1999) Effects of landuse on native fish communities in East Coast streams of the North Island of New Zealand. *N Z J Mar Freshwat Res* 33:141–151
- Rutledge MJ (1992) Survey of Chatham Island indigenous freshwater fish, November 1989. Department of Conservation, Christchurch, N Z, 21 pp
- Skrzynski W (1967) Freshwater fishes of the Chatham Islands. *N Z J Mar Freshwater Res* 1:89–98
- Smith PJ, Benson PG, Stanger C, Chisnall BK, Jellyman DG (2001) Genetic structure of New Zealand eels, *Anguilla dieffenbachii* and *A. australis*. *Ecol Freshwat Fish* 10:132–137
- Smith PJ, McVeagh SM, Allibone R (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 439–455
- Spiers D, Boubée J (1997) The effect of Ruapehu's ash on fish. *Fish Game N Z* 16:14–21
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123

- Tombs A (1960) Corrosion of metals in Whangaehu and Ruapehu crater waters. *N Z J Sci* 3:93–99
- Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Walker KF, Byrne M, Hickey CW, Roper DS (2001) Freshwater mussels (Hyriidae, Unionidae) of Australia. In: Bauer G, Wächter K (eds) *Ecology and evolution of the freshwater mussels Unionoida*. Springer, Berlin, Germany, pp 5–29
- Wallis GP, Trewick SA (2001) Finding fault with vicariance: a critique of Heads (1998). *Syst Biol* 50:602–609
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 3548–3580
- Walzl T (2006) Environmental impacts of the Tongariro Power Development Scheme. National Park Enquiry WAI 1130. Waitangi Tribunal, Wellington, N Z
- Wardle P (1963) Evolution and distribution of the New Zealand flora as affected by Quaternary climates. *N Z J Bot* 1:3–17
- Wardle P (1968) Evidence for a pre-Quaternary element in the mountain flora of New Zealand. *N Z J Bot* 6:120–125
- Wardle P (1978) Origin of the mountain flora with special reference to trans-Tasman relationships. *N Z J Bot* 16:535–550
- Waters JM, Wallis GP (2001a) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution* 55:587–597
- Waters JM, Wallis GP (2001b) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *J Fish Biol* 58:1166–1180
- Waters JM, Esa YB, Wallis GP (2001) Genetic and morphological evidence for reproductive isolation between sympatric populations of *Galaxias* (Teleostei: Galaxiidae) in South Island, New Zealand. *Biol J Linn Soc* 73:287–298
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid fish lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Whitehouse IE, Pearce AJ (1992) Shaping the mountains of New Zealand. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 144–160
- Williams K, Keys H (2008) Ruapeh erupts. Godwit, N Z, Auckland, 63 pp
- Willett RW (1950) The New Zealand Pleistocene snow line, climatic conditions, and suggested biological effects. *N Z J Sci Tech* 32B:18–48
- Wilson CJN (1993) Stratigraphy, chronology, styles and dynamics of late Quaternary eruptions from Taupo volcano, New Zealand. *Phil Trans R Soc Lond A343*:205–306
- Wilson CJN, Houghton BF (1993) The Taupo eruption. Institute of Geological and Nuclear Sciences, Taupo, N Z, 6 pp
- Wilson GDF (2008) Gondwanan groundwater connections of Australian phreatoicidean isopods (Crustacea) to India and New Zealand. *Invert Syst* 22:301–310
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Dive Evol* 8:237–247

Chapter 18

A Biogeographical Synthesis 3: Issues of Diadromy, Diversification and Dispersal

Abstract The presence of diadromy in the fauna provides an ability for restoration of fish populations to ecosystems perturbed by major, cataclysmic historical events like glaciation, volcanism and other geological occurrences, in a way that is not true of non-diadromous species. New Zealand has very few lake-limited or lake adapted species, probably because existing lakes are young, most of them being post-glacial to recent in age. As a result the distribution patterns of diadromous and non-diadromous species are very different. Dispersal through coastal seas results in diadromous species exhibiting very little genetic structuring in the way evident in non-diadromous species.

Keywords Diadromy • DNA sequencing • Dispersal • Genetic structuring • Glaciation • Restoration • Speciation • Volcanism

New Zealand's freshwater fish fauna exhibits patterns of diversification and distribution that relate to both ecological and historical events/influences spatially across the New Zealand landscape and temporally across geological time scales. In this chapter I explore some of the events involved and discuss some dichotomies driven by different behavioural/life history categories.

18.1 Failure to Disperse in a Dispersal Fauna

One of the enigmas in the distributions of the non-diadromous species has been their apparent failure to disperse – especially that they have not spread downstream in large rivers, and so there is an apparent, localised absence of dispersal in a fauna that other patterns suggest is a 'dispersal fauna'. A lack of upstream movement is perhaps intuitively/conceptually less surprising, but given their often free-swimming larval life stages, the lack of downstream dispersal in this fauna is somewhat surprising. In part, range extension may be restricted by environmental suitability, and perhaps in part by fish behaviour – some species may spread more easily as an

outcome of behaviour and other habits. Failure to disperse may be instances of what Mayr (1963); Mayr and Diamond (2001) labelled “philopatry”, a tendency for a species to stay in its native range, even though dispersal beyond that locality would seem to pose no difficulties. Mayr (1963) used the term for birds, where flight is involved in dispersal; downstream dispersal in fluvial habitats by fishes would seem an even easier process, physically, but clearly it often does not happen. Even within river systems, species’ actual ranges seem rather narrower than their potential ranges, but perhaps we don’t know enough to recognise what is limiting range.

Nevertheless, there has clearly been major spread by species, across New Zealand’s temporal/geological history, in response to the re-emergence of submerged landscapes, glacial advances and retreats, and the formation of land bridges that have sometimes connected the main islands of New Zealand. This suggests that strong philopatry across long time scales is unlikely, as there clearly must have been a great deal of local (re-)dispersal going on to establish fish populations in various areas – especially as the New Zealand landscape emerged after the Oligocene, and/or as the southern North Island emerged in the Pliocene, and/or as climate changed and glaciers retreated at the end of the last Pleistocene glacial period and the waterways of the intermontane valleys became inhabitable. Redispersion and reinvasion were probably especially rapid and predominant among diadromous species. But there are also numerous examples of freshwater fish species that are apparently ‘locked into’ upstream habitats, and which have failed to disperse downstream. Causes of the apparent lack of dispersal are unclear. The New Zealand freshwater fish fauna seems so impoverished, especially at the local, stream-reach scale, that it is counterintuitive to think that interspecific competition has been involved in a major way, though it may have been, locally. In some instances the absence of downstream spread, may be due to the lower reaches of rivers being too warm in summer for the upstream species to survive, but equally often this seems unlikely, given many species’ very broad contemporary ranges. However, there are few data on either river temperatures or species’ temperature preferences. Upland and Cran’s bullies seem to have achieved wider ranges in downstream habitats than many of the non-diadromous galaxiids.

Some examples of the lack of downstream dispersals and idiosyncratic distribution patterns are as follows:

- (i) Northern flathead galaxias seems to be restricted to only the upper reaches of the Maruia and Rappahannock tributaries of the west flowing Buller River (see Fig. 11.2, arrow 2), and is not known further downstream than these headwater streams. It also does not seem to have spread down the Motueka River from that river’s headwaters (see Fig. 11.2, arrow 1).
- (ii) Canterbury galaxias (see Fig. 11.2 – grey symbols), alpine galaxias (see Fig. 12.2 – green symbols) and upland longjaw galaxias (see Fig. 12.4 – black symbols) seem rarely to have spread far downstream from the intermontane valleys in the rivers of the Canterbury Plains; the reproductive status of occasional ‘plains’ individuals of these species is uncertain – they could be expatriates that do not survive for long and/or do not reproduce successfully;

certainly these individuals seem sparse and downstream populations do not build up.

- (iii) There are discrete 'upper' and 'lower' Taieri River galaxiid faunas: Taieri flathead (see Fig. 11.3 – red symbols) and Central Otago roundhead galaxias (see Fig. 11.2 – light green symbols) are found in the upper, Maniototo reaches of the Taieri catchment, and spread only as far downstream as about the towns of Middlemarch or Outram (see Fig. 11.2, arrow 11; Fig. 11.3, arrow 15;), but Eldon's and dusky galaxias are present in lower reaches of the system, and especially the Waipori River. However, there are no instances of co-occurrence of any of these lineages from the upper and lower Taieri (see Figs. 11.2, 11.3). However, dusky galaxias and Teviot flathead galaxias have both spread into the very headwaters of the upper Taieri River catchment, probably from some tributary of the Waipori River, but this must have been by a headwater capture event associated with Red Swamp Creek, while Taieri flatheads are present in other, nearby, upper Taieri tributaries.
- (iv) Regardless of how they are viewed, the populations of Taieri flathead galaxias, in the Akatore Stream, a small, independent coastal catchment near the mouth of the Taieri, and in the Narrowdale Stream, a tributary of the Tokomairiro, have to be enigmatic and these appear to result from some unusual, unidentified downstream dispersal events (see Fig. 11.3, arrows 12 and 13, Fig. 11.5, arrows 9 and 10); they could be the result of erratic dispersal processes, or they could be relicts surviving from a former broader range of a species that has retreated upstream in the Taieri River.
- (v) It seems paradoxical that although both Cran's and upland bullies have become widely distributed across the western-central North Island (see Fig. 15.2 – blue symbols), dwarf galaxias has not (see Fig. 12.2 – blue symbols).
- (vi) The apparent failure of *Neochanna* mudfish to penetrate south into Otago and Southland (see Fig. 14.3), when alpine galaxias (see Fig. 11.2 – green symbols) and upland bully (see Fig. 15.2 – blue symbols) both seem to have done so, implies that these two groups, though having very broadly overlapping ranges, have very different dispersal histories; a perhaps less parsimonious explanation might be that Otago/Southland once had a mudfish that was extirpated there, but there is no known hint of this.
- (vii) The absence of upland bully from the Nevis and Von Rivers, is a stark contrast with Gollum galaxias and southern flathead galaxias being variously present, presumably having entered the Nevis from the Mataura and the Von from the upper Oreti prior to, or since, their flow reversals took place (Waters et al. 2001; Burridge et al. 2006). Also, although present in the Nevis, Gollum galaxias seem to have failed to spread downstream from the Nevis and into the Kawarau.
- (viii) Failure of southern flatheads to spread downstream in the Mataura (see Fig. 11.2 – black symbols), though Gollum galaxias is widespread there (see Fig. 11.3 – green symbols) seems inexplicable, especially given that both species are found widely throughout other Southland rivers.

It has to be accepted that there has been substantial dispersal of various freshwater fish lineages around a wide area of the southeastern South Island in relation to climatic and geological changes. The *Gl. vulgaris* species complex and pencil-galaxias species of the eastern South Island, and upland bully, if they were formerly present there, would almost certainly have been driven out of the larger intermontane river basins of the eastern Southern Alps, and downstream onto the formative plains, at the last glacial advance when the intermontane valleys of the eastern flanks of the Southern Alps were filled with ice (though perhaps not driven entirely from the Mackenzie basin of the upper Waitaki River, depending on how extensive glacial advances were there – Fitzharris et al. 1992). Whether or not they were there to be driven out by the glacial advance, they have certainly (re-)invaded the eastern-flowing rivers draining these intermontane valleys very widely, since glacial retreat. Presence of these lineages in rivers of the nascent plains during the Pleistocene may have been pivotal in facilitating their widespread presence across the eastern and southern South Island, as well as being the source of populations now found in the intermontane valleys.

It is clear that there has been continual and very substantial re-dispersal of non-diadromous fishes around New Zealand as landscape and climate have changed, but in ways distinctive for each species group across geological time. The diadromous species do it all the time at the cohort scale. An implication of this pervasive dispersal is that distribution patterns are only in small measure a function of geological history.

18.2 Idiosyncratic Distributions of Non-diadromous Species

Viewed on a broad spatial scale, individual species and species groups exhibit patterns of distribution that are diverse and idiosyncratic. Some non-diadromous taxa have very broad ranges across the landscape (Canterbury galaxias, dwarf galaxias, upland bully, Cran's bully), whereas other related species are very localised (such as burgundy mudfish and Tarndale bully). Moreover, there has been substantial diversification in the southern South Island by the *Galaxias vulgaris* species complex and in the McKenzie Basin by the pencil-galaxias complex, whereas only a single species is presently recognised across this area (and much more widely) in upland bully. There are also, however, some similarities in detail, especially the presence of some species on both sides of Cook Strait (dwarf galaxias, brown mudfish, upland bully) and Foveaux Strait (southern flathead, Gollum galaxias, upland bully). Another common pattern is the absence of any non-diadromous species south of Okarito on the West Coast. What is paramount is that patterns in each species group are distinctive both as individual species' ranges, and as patterns of sympatry and/or overlap. It is inescapable that each complex has responded distinctively to past geomorphological events especially across the southern North Island and the South Island – there are no simple or universal patterns.

18.3 Responses of Diadromous Fishes to Major Recent Natural Perturbations (Land Connections, Volcanism and the Pleistocene Ice Ages)

Inspection of the geographical ranges of diadromous species gives no hint that their patterns relate in any way to New Zealand's geological history – they tend to be very widespread around New Zealand and areas of absence seem to relate to one, or more, of habitat unsuitability, difficulties in recruitment, and a lack of access for fish migrating into rivers from the sea – there are proximate barriers to upstream spread that affect patterns at the cohort scale. As well, of course, species' ranges are determined by migratory instincts and capabilities. There must have been severe impacts from major volcanic eruptions at various, quite recent times (Holocene) – around Auckland, across the Taupo-Rotorua volcanic zone and to the north-east (McDowall 1996b), and in the rivers of the ring plain around the slopes of Mount Taranaki (Neall 1992; Alloway et al. 1995), but these rivers now have diverse diadromous species that have clearly been able to reinvade them since the adverse impacts of volcanic activity became dissipated. Diadromous species are also widespread along the West Coast of the South Island, including river systems within the 'beech gap' where it is believed that glacial ice covered the landscape to beyond the present West Coast coastline during the last (Otiran) glacial advance (see Fig. 3.4) (Main 1989; McDowall 1996b), and where it is likely that all aquatic life was obliterated as a result; valleys were ice filled and stream flows possibly starved of water, especially in winter, by precipitation being locked up as ice/snow accumulations in the mountain valleys. Again, most of New Zealand's diadromous species are now widely present there, and this is a probable outcome of their ability to move into rivers from the sea. This includes very wide presence of koaro now landlocked in numerous sub-montane and montane lakes that derive from post-glacial invasion.

18.4 Residual Effects of Volcanism on Lake Populations of Fishes

Some New Zealand lakes were/are profoundly influenced by Recent volcanism, primarily lakes of the central North Island – especially Lakes Taupo, Rotoaira and Rotopounamu, and no doubt others, in relation to the very long series of major Taupo eruptions, Lakes Rotomahana and Tarawera were affected very recently as a consequence of the 1886 Mount Tarawera eruption, though that was relatively minor compared with the long series of very major eruptions across the central North Island during the last 50,000 years. There are landlocked populations of common smelt, koaro and common bullies in many of the lakes of the central/eastern North Island, despite all of these lakes almost certainly being severely perturbed by repeated volcanic activity extending into relatively recent times (<2,000 BP). Mair

(Crosby 2004) described the water of Lake Rotomahana as being “...the colour of pea soup...” after the eruption of Mt. Tarawera in 1886, and this provides some hint of the likely impacts of the various, earlier Taupo eruptions on various of the other lakes. Reed (1952) speculated that freshwater mussels (*Echyridella* sp.) were exterminated from Rotomahana by the Tarawera eruption, and he was probably correct. If so, fish now present in the lakes would have been also. It is possible that fish like koaro found their way into some of the central North Island lakes, by stream headwater captures into Lake Taupo, perhaps from the upper Whanganui, Rangitikei or Rangitaiki Rivers – though the likelihood of this happening has never been explicitly investigated, and we will probably never know.

It is thought likely that fish in some of the lakes of the area were introduced in historic times by the Maori people, for whom there is a tradition of fish translocation (Fletcher 1919; Best 1929; Andersen 1942; Stafford 1967; McDowall *in press*). Thus the fish populations in some of these inland lakes may reflect translocations by Maori who lived around the lakes. Maori legends point to a traditional role in Maori translocation (Anon 1942; Tapsell 1972; Taiaroa-Smithies and Taiaroa 2006). That point aside, the conclusion is inescapable that the altitudinal and penetration ranges for riverine populations of diadromous species in general tend to be much lower than the distances inland of many conspecific lake populations. This, among other things, clearly demonstrates that the upstream range limits of these normally diadromous species are not determined by features of proximate habitat quality such as temperature, so much perhaps as by the ability of these species to reach these habitats at an on-going, proximate, cohort-level, temporal scale. It begs the question of how the more inland/high elevation lake populations became established, and the only logical answer is that, apart from the possibility of historical Polynesian Maori translocations, diadromous species must, at times, (perhaps only once in each lake), have penetrated upstream far enough to allow their entry to these lakes where non-migratory populations then became established. Molecular studies might be interesting to determine whether there is very low genetic diversity in the lake populations that would be consistent with establishment of these populations from very small propagules.

18.5 Penetration by Diadromous Species Though Lakes

Some diadromous species that do not seem to have the ability to establish lake-limited populations are nevertheless found in swiftly-flowing, coarse substrate, cobble/boulder stream habitats upstream of lakes (especially torrentfish and bluegill bully). These species live in the most swiftly-flowing habitats available in New Zealand rivers, and yet populations of some of them are found upstream of substantial lakes; e.g. torrentfish is present in the Tauherenikau River (at the upstream end of Lake Wairarapa: Fig. 18.1, arrow 1), to reach which the fish must have swum up the length of Lake Onoke, then up a meandering, sandy-bedded

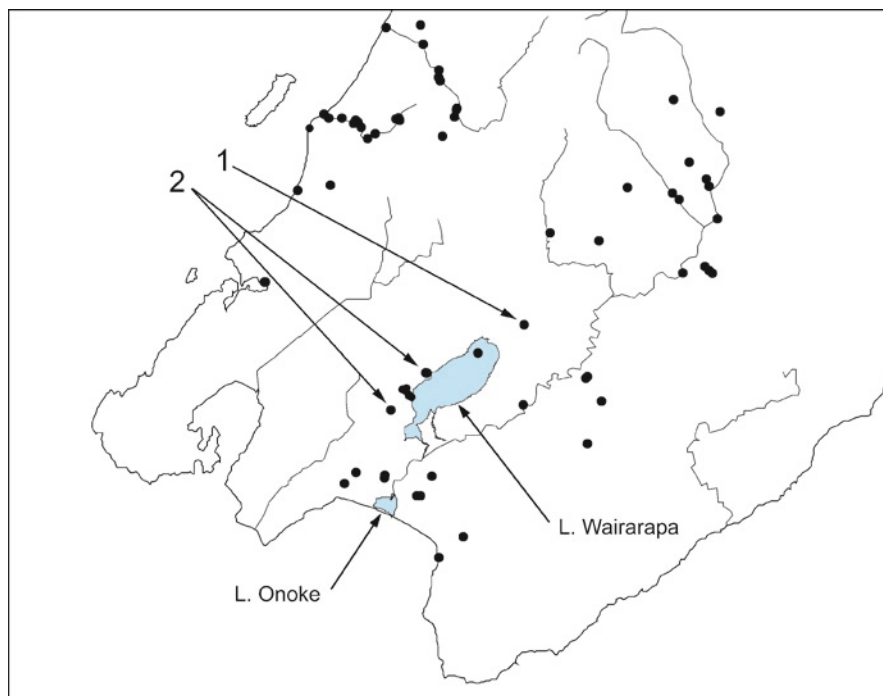


Fig. 18.1 Penetration upstream by torrentfish, *Cheimarrichthys fosteri*, and bluegill bully, *Gobiomorphus hubbsi*, through Lakes Onoke and Wairarapa in the southern North Island. **Arrows** – ↑1: torrentfish in the Tauherenikau River above Lake Wairarapa; ↑2: torrentfish and bluegill bully in tributaries of the lower reaches of the lake

river, and finally up a sandy lake shore/bed – a minimum of 41 km. Bluegill bully is found in a tributary of the same lake involving upstream movement of 27 km from the sea, again requiring them to swim through lacustrine or gently-flowing, meandering riverine habitats. To reach the Selwyn and L2 Rivers (Fig. 18.1, arrow 2), torrentfish must swim at least 25 km across (or further if it was around the shores of) Lake Ellesmere (Fig. 18.2, arrow 2). Moreover, the torrentfish is known in the Ryton River, a tributary of Lake Coleridge, to reach which it must first have migrated 142 km up the swiftly-flowing Rakaia and Wilberforce Rivers (to reach an elevation of 504 m), have entered Lake Coleridge via its outlet stream, and then have swum around the shores of the lake for a distance of ca. 10 km (Fig. 18.2, arrow 1). In none of these extremes is the migratory species abundant, but penetration through these lakes involves substantial distances by species across habitats that they probably would not have been predicted to be capable of. These observations are interesting, given discussion, above, about the presence of non-diadromous species present upstream of glacial lakes in the Mackenzie Basin (Chapter 17).

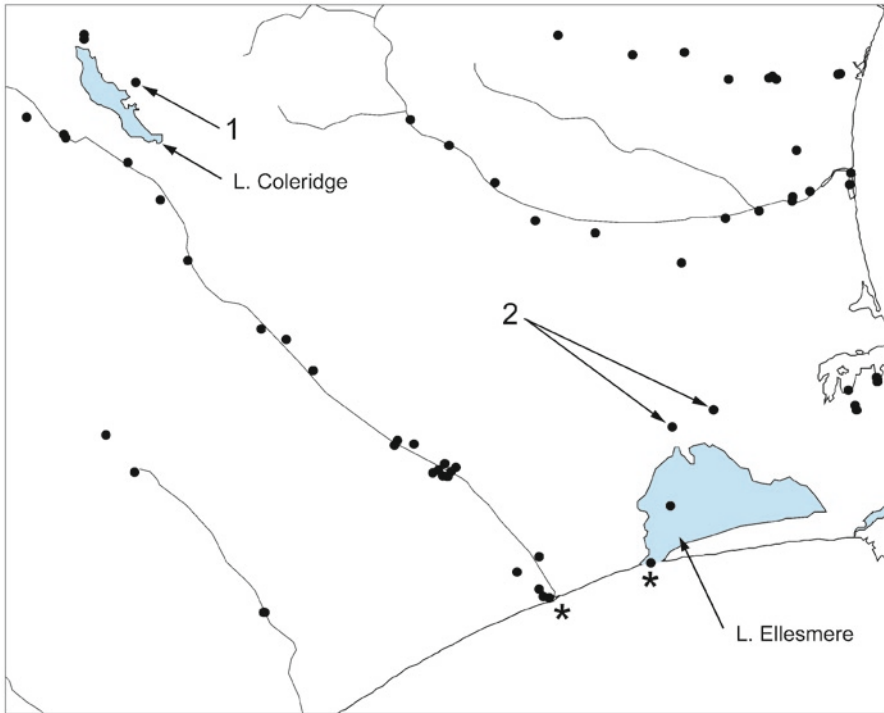


Fig. 18.2 Penetration upstream by torrentfish, *Cheimarrichthys fosteri*, and bluegill bully, *Gobiomorphus hubbsi*, through the Rakaia River and Lake Coleridge and through Lake Ellesmere into the Selwyn River a major tributary of that lake in the eastern South Island. **Arrows** – ↑1: Lake Coleridge; ↑2: above Lake Ellesmere

18.6 High Inland Penetration by Weak Diadromous Migrants

It does not automatically follow that those diadromous species that appear to be among the weaker inland migrants, are necessarily restricted to sites in rivers short distances inland from the sea. Distance, per se, may not be a strong impediment to penetration. There are some instances of surprisingly high inland penetration by species, such as common smelt and inanga, that other general data suggest are among the weaker upstream migrants. These instances are notably in river systems of very low gradient: e.g.,

(i) Common smelt is present:

- 217 km up the Waikato River (but it reaches an elevation of only 50 m in doing so)
- 153 km up the Waihou River (90 m elevation)
- 270 km up the Whanganui River (200 m elevation)
- 182 km up the Manawatu River (elevation 290 m)

(ii) Inanga is known:

- 208 km up the Waikato River (62 m elevation)
- 218 km up the Whanganui River (120 m)
- 146 km up the Manawatu River (320 m)

For some of these data the relationship between distance inland and elevation for the two species may seem mutually inconsistent, i.e. how could common smelt reach 182 km up the Manawatu River to reach an elevation of 290 m, whereas inanga penetrates only 146 km but reaches an elevation of 320 m. This is caused, in part, by maximum elevation and distance reached by fish sometimes involving different tributaries of the named rivers. There are similar data for other species. As well, however, there are species that do not ever move far upstream, regardless of river gradient, e.g. Stokell's smelt, no more than 12 km (9 m elevation) (see Figs 9.7c, 10.1) and giant bully 21 km (30 m) (see Fig. 9.7h) (McDowall 2000).

18.7 The Role of Lakes and Wetlands in the Evolutionary Ecology of New Zealand Freshwater Fishes

New Zealand has many hundreds of lakes, varying from the large Lake Taupo (area 623 km²) in the central North Island, to masses of small wetlands, lagoons and mountain tarns (Irwin 1975; Lowe and Green 1987, 1992; Cromarty and Scott 1996). Despite this abundance of lakes, the lacustrine fish fauna of New Zealand exhibits very low species diversity and is derived largely from riverine fishes. Species endemic to lakes are restricted to:

- (i) Dune lakes galaxias in a few small coastal and lowland lakes in Northland (see Fig. 13.2 – red symbols) (Chapter 13)
- (ii) Tarndale bully found in several small sub-montane lakes in the saddle between the headwaters of the Wairau and Clarence Rivers in inland Marlborough (see Figs 15.2, 15.3) (Chapter 15)
- (iii) Chatham mudfish in two small lakes in the south of Chatham Island (see Fig. 14.3 – green symbols, arrow 21) (Chapter 14)

Interestingly, in all three species the lakes involved are really small (the largest is L. Taharoa in Northland which has area of only 2.1 km², and all others are less than 1 km² in area (Irwin 1975). This might seem counter-intuitive, i.e., it might be expected that species would be found in large lakes, and in lakes that would tend to be older and/or have a longer life span. The likely explanation is that most large lakes in New Zealand are also all very young, being formed either from Pleistocene glaciation, Holocene/Recent volcanism, or by Recent earthquake-driven landslides (Irwin 1975; Adams 1981; Lowe and Green 1987, 1992). Thus, there are few lakes of great age in New Zealand within which local endemics could have evolved. The

presence of fossils associated with Palaeo-lake(s) Manuherikia and in another small maar in Central Otago (see [Section 1.8](#)), some of which clearly seem to be of species different from the extant fauna, indicates the likelihood of former greater diversity in the lake faunas (McDowall 1976; McDowall and Pole 1997; McDowall and Lee 2005; McDowall et al. 2006a, b; Lee et al. 2007) that has failed to persist, perhaps owing to these lakes disappearing and their fish faunas with them – just as has happened in Central Otago (Douglas 1986); or in a Pleistocene Palaeolake at Ormond, in the Waipaoa River Valley in the northeastern North Island, from which fossil *Gobiomorphus* and *Prototroctes* have been described (McDowall et al. 2006a, b).

The fish faunas in New Zealand's contemporary lakes thus typically consist of landlocked stocks of diadromous species that have been able to make their way upstream to reach the various lakes – mostly common smelt, common bully, koaro, less often banded kokopu, giant kokopu, and, occasionally, inanga. These upstream movements may have been one-off events in each lake, they could have happened repeatedly in some, or they may even still be happening repeatedly or sporadically in others. Again, how many of these fish populations are naturally established in the lakes, as opposed to resulting from translocations by ancient Maori or more contemporary European settlers, is unknown – though all of these processes may have played a part in the development of the lakes' present fish faunas.

18.8 Lowland Species in Upland Lakes

A paradoxical aspect of the distributions of lake populations of otherwise diadromous species is that often, landlocked populations of these species are found in lakes much further inland, and at higher elevations, than the upstream limits of their diadromous conspecific populations in the same river catchments. Examples include the following populations of common smelt:

- (i) In Lake Sumner, 114 km up the Hurunui River from its mouth, and at an elevation of 525 m (Fig. 18.3a, arrow 6); whereas diadromous stocks are reported only from the river's estuary (0 km upstream).
- (ii) In Lake Heron, 157 km up the Rakaia River (Fig. 18.3a, arrow 5), and at an elevation of 695 m, otherwise present only in the estuary of that river (0.1 km upstream).
- (iii) In a small un-named pond near Lake Ohau, 160 km up the Waitaki River and at an elevation of 520 m (Fig. 18.3a, arrow 4), but it is found only up to 1 m elevation in the mainstem of the river from the sea (1.4 km upstream – though it is possible that this lake population derives from an undocumented human translocation).
- (iv) In several lakes in the Waiau River: Lake Thomas 135 km up the Waiau elevation 490 m (Fig 18.3a, arrow 3), Lake Henry at 149 km and 205 m and Lake Te Anau 170 km and 202 m (Fig 18.3a, arrow 2), whereas in the Waiau River this species reaches 105 km and elevation 175 m.

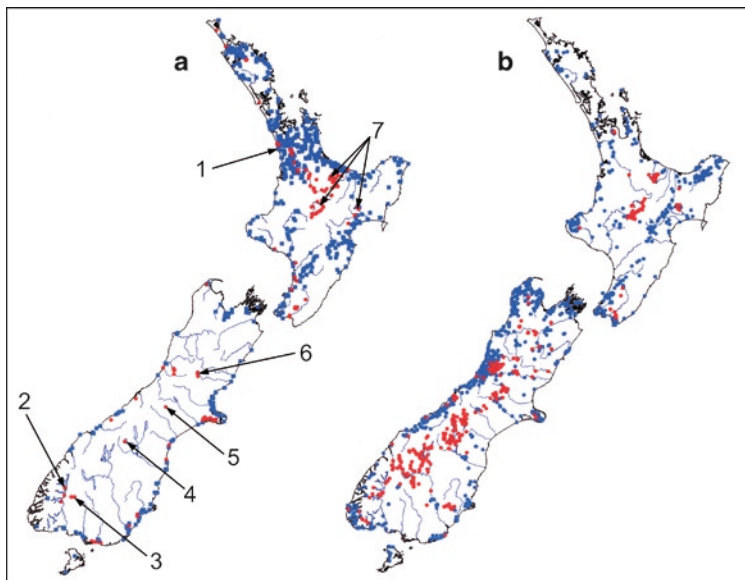


Fig. 18.3 Diadromous (■) and landlocked (■) populations of a. koaro, *Galaxias brevipinnis*; b. common smelt, *Retropinna retropinna*. **Arrows** – ↑1: populations spread down from upstream lakes; ↑2: lakes near Te Anau; ↑3: Lake Thomas; ↑4: tarn near Lake Ohau; ↑5: Lake Heron; ↑6: Lake Sumner; ↑7: lakes of the central North Island, many populations resulting from human translocations (note much greater inland spread of landlocked populations in most species)

Similar data are available for giant kokopu which is present:

- (v) In Lake Luxmore that is 128 km upstream and at elevation 370 m, in Lake Mistletoe 178 km upstream and at 205 m elevation, and in Lake Monowai that is 83 km upstream and at an elevation 190 m, all in the Waiau River system (Southland), although there are actually no records of diadromous stocks of this species from the Waiau, at all.

Comparable data could be presented for additional diadromous species, especially for common bully, banded kokopu and koaro – though, for the last of these, contrasts between the elevations of lacustrine and diadromous stocks are somewhat less decisive owing to the ability of diadromous individuals of koaro to migrate upstream very long distances and up steep gradients and falls.

These apparent discrepancies basically show that what has sometimes happened across history is not being repeated at contemporary time scales.

18.9 Evolutionary History and the Loss of Diadromy

An understanding of the phylogenetic relationships of the New Zealand freshwater fish fauna points to a repeated role for the loss of diadromy in contributing to taxonomic diversity and species' distributions patterns. Molecular studies are revealing

a series of instances in which non-diadromous species have an ancestry shared with diadromous species, discussed above, and views dating back to McDowall (1970). (Repeated loss of diadromy in galaxiid fishes is also said to have played a similar, major role in the cladogenesis of the Australian Galaxiidae – McDowall and Frankenberg 1981; Ovenden and White 1990; Raadik 2001). New Zealand instances include the following:

- The non-diadromous dune lakes galaxias was originally described as a landlocked derivative of the diadromous inanga (McDowall 1967), and later molecular studies have supported this view – though the patterns of derivation in the various lakes where this fish is found (see Fig. 13.2) may not be simple and there may be multiple derivations in different lakes, or groups of associated lakes from a common ancestor (Ling et al. 2001).
- The species of the *Gl. vulgaris* species group have long been regarded as fluvial derivatives of the diadromous koaro (McDowall 1970), either several times (Waters and Wallis 2001) or perhaps only once (Waters et al. in press).
- New Zealand's *Neochanna* mudfishes appear probably derived from the diadromous Tasmanian mudfish (McDowall 1997, 2004; Waters and White 1997; Waters and McDowall 2005).
- The Tarndale bully seems clearly to be a landlocked derivative of common bully, whereas the non-diadromous upland bully and Cran's bully have been shown to share separate and complex ancestries with other diadromous *Gobiomorphus* species (McDowall 1994; Smith et al. 2003; McDowall and Stevens 2007; Stevens and Hicks 2009). Upland bully shares a common ancestry with a clade comprising redfin and giant bully, whereas Tarndale bully and common bully form a clade that shares a common ancestry with Cran's bully. Bluegill bully is basal to the entire New Zealand radiation (Stevens and Hicks 2009).

Thus, loss of diadromy associated with speciation is clearly a significant aspect of the evolutionary history and biogeography of the fauna across a diversity of taxonomic groups and geographical ranges. The ancestries of other non-diadromous *Galaxias* species, e.g. the pencil-galaxias complex – alpine, bignose, dwarf, lowland and upland longjaw galaxias – are presently unknown.

At times, the abandonment of diadromy has been enforced by physical changes to river systems that prevent migrations to and from the sea – as when lakes are formed by landslides (Lakes Waikaremoana, in the northeastern North Island, Chalice in Marlborough, and Christabel in inland West Coast), or when lake outlets become blocked by coastal drift of gravels or sand, or other events (Lake Wahakari, Kai Iwi Lakes, Poutu Lakes in Northland – see Fig. 13.2 – red symbols; Ellesmere and Forsyth near Banks Peninsula, the Kaihoka Lakes in the far north-western South Island, Horseshoe Lagoon in mid-Canterbury; Waituna Lagoon in Southland; Te Whanga Lagoon on Chatham Island; and others). Populations of otherwise diadromous species have become trapped in these lakes and have had to

abandon their diadromous migrations, or be present only intermittently following occasional instances of lake outlet opening that coincide with immigration periods for the juveniles of the various species found in the lakes. Species involved include common smelt, banded kokopu, giant kokopu, koaro, inanga, and especially common bully.

In addition, there are numerous instances of the establishment of lake populations of diadromous species when there is no obvious physical impediment to migration between lakes and the sea. It is uncertain whether the absence of diadromy in these populations is a 'tactical life history choice' by the population, or is due simply to the larvae failing to find their way to lake outlets and thus they have not become entrained in rivers discharging from lakes to sea. And there are some, perhaps many, instances in which conspecific diadromous and non-diadromous populations co-occur in lakes, as with common smelt – the lower Waikato lakes, Lakes Wairarapa, Forsyth and Ellesmere, perhaps Waituna Lagoon, and probably others (McDowall 1979, 1990; Northcote and Ward 1985; Northcote et al. 1992). This has also been shown to be true for giant kokopu in the lower Taieri lakes (Waiholo, Waipori) in the southeastern South Island, based on the study otolith microchemistry (David et al. 2004) and is probably true for banded kokopu in lakes of the lower Waikato River (Hicks et al. 2008), and for both giant kokopu and banded kokopu in Waituna Lagoon.

Sometimes the populations established in lakes develop a pattern of migrations between lakes and their tributaries that mirrors the pattern of migration between the sea and river systems (McDowall 1990). Larval life among the marine plankton in diadromous populations replaced by larval life in the pelagic zone of lakes. In addition, at least in koaro, there may be vigorous seasonal migrations of the whitebait-like juveniles from the lakes into the lake tributaries (McDowall 1970, 1984) – though this is by no means always true of that species, and the adults may be entirely lacustrine in habit (Young 2002; King et al. 2003). This is probably less often true of other lake populations of diadromous *Galaxias* species – banded and giant kokopu, common bully and common smelt in lakes tend to be entirely lacustrine with larvae, juveniles of all species, and even adult smelt, being pelagic, though in the other species, the adults become benthic and littoral.

Some aspects of the migration patterns of diadromous species are still emerging. It appears, for instance, that in some river systems, diadromy may be highly facultative, at least in common bully and perhaps also giant kokopu. Studies of the chemical composition of otoliths in these two species are suggesting that some individuals in riverine populations have never been to sea (Closs et al. 2003; David et al. 2004); again, the nature of this life history variation, and what is driving it, are unknown. Larvae could be being entrained along riparian margins of rivers, or may be unable to find their way out of lagoons or ponds and into rivers as well-grown juveniles or sub-adults. Whatever happens, sparseness of very small foods suitable for the very small larvae of these diadromous species among those that do not go to sea, may result in high larval mortalities, especially along river margins.

18.10 Durability of Wetland Fish Populations – Taranaki Volcanism and West Coast Glaciation

There are hints that wetland populations of freshwater fish may be less vulnerable to extirpation under extreme conditions, or perturbations, than fluvial populations, involving: brown mudfish in wetlands to the west of Mount Taranaki where upland and Cran's bullies are absent; also, the extended southern range of brown mudfish as far as Okarito in the West Coast (see Fig. 14.3, arrow 8 – brown symbols), and thus further south into the area implicated by Pleistocene glaciation (the beech gap), than is true of either dwarf galaxias (see Fig. 12.2, arrow 8) or upland bully (see Fig. 15.2, arrow 8) (both spreading south only as far as the Hokitika River. It is uncertain whether the brown mudfish has been able survive these perturbations in isolated wetland fragments when other non-diadromous species have not, or alternatively whether it has been better able to reinvade affected areas since amelioration of the effects of climate and the impacts of the most recent volcanism on these freshwater habitats. Perhaps fluvial habitats occupied by other fish were more severely impacted, than the wetlands pockets where brown mudfish is present, owing to their vulnerability to the downstream impacts of upstream perturbations, as when ash deposits were flushed down stream during episodes of elevated flows. Or, is it possible that the small fragmented wetland habitats where brown mudfish is found, may have provided some protection of the species' populations from the impacts of erosion of volcanic discharges or glaciation? Certainly the presence of mudfish in both impacted areas is of distinctive interest.

18.11 Issues of Genetic Structuring

Several studies have shown that diadromous New Zealand fishes tend to exhibit a lack of genetic structuring across their broad geographical ranges.

- Barker and Lambert (1988) found no genetic structuring in diadromous inanga. Similarly, Dijkstra (1999) and Waters et al. (2000) concluded that, in the diadromous inanga, despite the identification of a very high level of haplotype diversity (Fig. 18.4), there is no geographically-based, genetic structuring at all, and the New Zealand stocks of this species are regarded as more or less panmictic. Zattara and Premoli (2005), in Chile, also found no genetic structuring in riverine, diadromous populations of inanga, though there was substantial genetic structuring in landlocked populations in Patagonian lakes – no doubt a consequence of the genetic/reproductive isolation of the lake populations resulting from loss of diadromy.
- Allibone and Wallis (1993) found no such structuring across a range of diadromous New Zealand galaxiids.
- Also, Dijkstra and Jellyman (1999) found no molecular evidence for separation of the two subspecies of shortfin eel sometimes recognised in Australia and

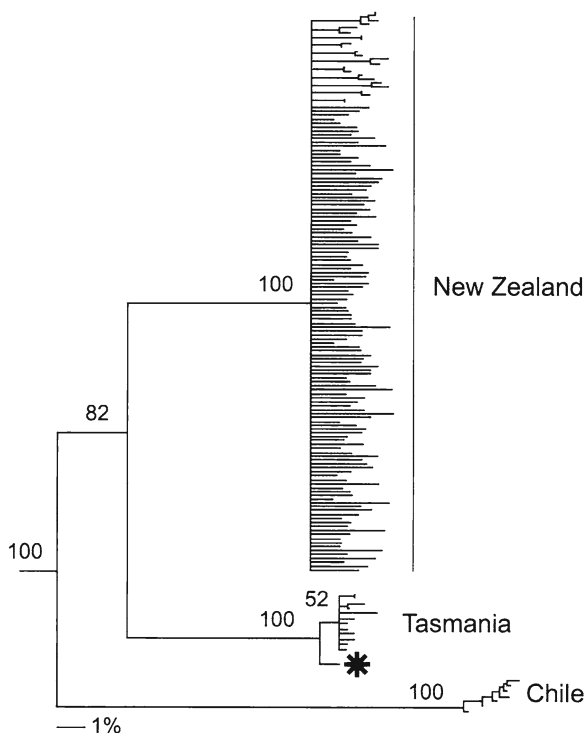


Fig. 18.4 Neighbour joining bootstrap phylogram from control region sequences in inanga, *Galaxias maculatus*, in which there is a very large number of haplotypes from New Zealand specimens; one Tasmanian haplotype (*) is also present in New Zealand (from Waters et al., 2000)

New Zealand (Schmidt 1928; Griffin 1936), nor evidence for genetic structuring across the species' New Zealand range. Smith et al. (2001) found that in both shortfin or longfin eels in New Zealand there is no genetic structure, which is consistent with a single, offshore spawning ground. Reference to the single spawning ground is the key element here as what happens there is pivotal to the development of genetic structuring across the latitudes of New Zealand, no matter how widespread the species. Both species are regarded as panmictic in New Zealand, and in the shortfin eel across the Tasman Sea as well, and that again must reflect what happens on the spawning grounds, not what happens in New Zealand (or Australian) rivers.

Similar questions have not been explored for diadromous bullies or torrentfish, but seem likely to provide similar answers: a lack of structuring across broad geographical ranges.

These results for galaxiids and eels are comparable with work published elsewhere on other groups of diadromous fishes, which has demonstrated a lack of genetic structuring globally across the ranges of a variety of diadromous fish

groups. (Gyllenstein 1985; Brown et al. 1993; Ward et al. 1994; Zink et al. 1996; Maes and Volckaert 2002; Berrebi et al. 2005; Keith et al. 2005; Hoareau et al. 2006). Clearly oceanic/coastal dispersal is an important aspect of the ecologies and genetics of diadromous species, in New Zealand and globally. Lucas and Baras (2001) also reported reduced genetic differentiation of peripheral fish species (in the sense of Darlington 1957) between river basins. Looking at an even broader taxonomic scale, Baker (1991) reported a lack of structuring in sea birds of the New Zealand region and attributed this, as in diadromous fishes, to their great dispersal ability, which he considered was translated into “realized gene flow”. Similarly, Greve et al. (2005: 162) stated that “Highly mobile taxa such as sea birds...have demonstrably panmictic populations” around the Southern Ocean. Thus patterns of genetic differentiation across widely-ranging taxa of a wide variety of taxa conform to a predictable pattern.

Diadromy thus promotes both broad geographical ranges and facilitates gene flow across the ranges of individual, diadromous fish taxa. In doing so diadromy may counteract local adaptation, and tend to obstruct or obscure evolutionary/speciation processes at geological time scales – though where there is homing by individuals back to their natal waters, this may counteract gene flow between populations (McDowall 2001). Homing has not been demonstrated for any New Zealand freshwater fish species, and seems intuitively unlikely, especially for amphidromous species, given how small they are at emigration to sea and how little time they spend in fresh water before doing so. They seem unlikely to have had time to imprint on the characteristics of their natal habitat. Meanwhile, an implication of this capacity to disperse among diadromous species is the capacity it provides for recovery from perturbation, and for the invasion of newly available habitats (McDowall 1996a, 1998). There are adaptive costs, however, since the gene flow provided by dispersal will impede the development of local adaptation in diadromous fishes (McDowall 2001)

This contrasts with the situation in non-diadromous species, in which there are much more complex, much narrower, and locally idiosyncratic distribution patterns, much higher genetic structuring within lineages, and common allopatry of related taxa; these imply a lack of gene flow that may be crucial in permitting speciation and taxonomic differentiation (Wallis et al. 2001 – *G. vulgaris* species complex; Davey et al. 2003 – Canterbury mudfish; Smith et al. 2005 – upland bully; Waters et al. 2006 – dwarf galaxias). The absence of diadromy restricts gene flow among populations, and this, in turn, facilitates local adaptation, divergence and speciation. However, at the same time, it restricts the ability of the species to be restored in sites where there has been local extirpation, or limits their ability to occupy newly available habitats (Milner 1987; Milner and Bailey 1989; McDowall 1996a, b, 2001) – they have much restricted ability to reach such newly available habitats through coastal seas.

A lack of genetic structuring across the very broad geographical ranges of diadromous species, compared with higher structuring in much more locally-distributed non-diadromous species, may seem counterintuitive, until it is recognised that dispersal through coastal seas, across the ranges of diadromous species, both results in broad ranges and facilitates the gene flow that destroys or inhibits structuring.

18.12 Several Widely Accepted Truisms

This book presents a distinctive perspective on biogeography through explicitly separating, comparing, and contrasting the roles of ecology and history in the macroecology and biogeography of the fauna – very much a ‘bottom up’ approach. Several ‘accepted truths’ are contradicted by the patterns explored here:

- One of these relates to the question of range size: nearly half the species in the fauna (the diadromous ones) have extensive, New Zealand-wide ranges, contrary to biogeographical/macroecological theory that suggests that most species in a fauna usually have narrow, rather than broad, geographical ranges (Gaston 1990, 2003a, b; Brown et al. 1996).
- Another ‘truism’ is that ecological issues are generally thought to influence patterns at a more local scale than geological ones (Humphries 2004): but here we have seen that the broad-scale distributions of New Zealand’s diadromous fish species, even for species found beyond New Zealand, are influenced very largely by ecological/behavioural processes (migration to and from the sea), whereas non-diadromous ones, which usually have much narrower ranges, are subject to more influence by local geological processes.
- As well, although species diversity is routinely regarded as being greater at the tropical ends of geographical continua, this does not apply to New Zealand freshwater fishes – in which diversity is greatest to the south, this being a probable outcome of local spatial-scale geological processes across Cenozoic-long time scales, rather than relating to some kind of historical/ecological continuum.

18.13 Range Disjunctions

There is a little evidence among New Zealand’s non-diadromous freshwater fishes for major geographic disjunctions within species’ ranges. There are two northern isolates of dwarf galaxias (Waihou and Rangitaiki Rivers) north of the central North Island volcanic zone (see Fig. 12.2, arrows 1 and 20), a species otherwise found only south of the zone, and this is a disjunction that resulted from volcanism at Lake Taupo, and there is another isolate in headwater tributaries of the Rangitikei River on the western slopes of the Ruahine Ranges (see Fig. 12.2, arrow 2), that probably reflects an old headwater stream capture. A population of alpine galaxias in the headwaters of the Manuhirikia River of Central Otago (see Fig. 12.2, arrow 13) is quite disjunct from other populations of that species elsewhere in the Clutha River system, and may be connected to (derived from) alpine galaxias populations in the nearby upper Ahuriri River (Waitaki River system) in the Mackenzie Basin. In addition, as discussed earlier, there are the populations of Taieri flathead galaxias in the Narrowdale, which is a low elevation tributary of the Tokomairiro River, and in a tributary of the lower Akatore Stream near the mouth of the Taieri, discussed above (see Fig. 11.3, arrows 12 and 13; Fig. 11.5, arrows 9 and 10); these

are a total enigma (though the mutual close proximity of these two disjunct populations may hint that there is a common causal explanation for both populations). Otherwise, and in general, patterns for non-diadromous species are cohesive and seem to have explanations that relate to landscape history.

It might be expected that elements in the freshwater fish fauna, whose geographical ranges are controlled by known geographical features or hypothesised vicariance events, ought to exhibit common disjunctions, i.e., different species might exhibit similar responses to the same landscape events/changes. There seem to be few such examples. One is the common presence of both Central Otago roundhead galaxias (*Gl. anomalus*) and Taieri flathead galaxias (*Gl. depressiceps*) in the upper Taieri but neither present in the lower Taieri. Two lineages (Teviot flathead and dusky galaxias) seem to have escaped from the mid-Clutha to be present in Red Swamp Creek (see [Sections 11.2.6 and 11.2.9](#)) in the uppermost Taieri.

The taxonomic diversity of the *Gl. vulgaris* species and pencil-galaxias complexes across the eastern South Island is a stark contrast with the scenario in upland bully, in which just a single species is recognised across the same broad area. And there is the commonality of both southern flatheads and Gollum galaxias being involved in stream capture in the Von, shifting them both into the Clutha catchment (Burridge et al. 2006 – though the presence of the two species in the Von may result from dual stream capture events. Moreover, despite these rather minor commonalities, other eastern South Islands species have distributions that give no hint of being affected by the same aspects of geographical history and river connectedness, e.g., alpine galaxias spreads across the Waitaki River basin and south as far as some of the upper tributaries of rivers of the Southland Plains (Waiau and Oreti Rivers) (see [Fig. 12.2](#), arrows 10 and 11), whereas upland bully spreads across the Waitaki and Clutha River systems, and is present throughout Southland (see [Fig. 15.2](#), arrow 11; [Fig. 15.7](#)) and beyond into the rivers of Stewart Island (see [Fig. 15.2](#), arrow 10). In general, although it is possible to identify what appear to be associations between the distribution patterns of closely related species, these patterns in general fail to apply across different species groups.

18.14 Species' Ranges and Environmental Suitability

The extent to which species' ranges equate with their environmental tolerances is poorly understood, i.e. it is often not clear whether individual species' range limits are due to:

1. Habitat suitability factors
2. To the ability/inability of fish to spread across the landscape
3. To past events that cause local extirpation and an inability to re-establish

In a history of fluctuating mid-late Cenozoic climates in New Zealand, non-diadromous taxa will probably have tended to move north and south, and/or downslope and upslope, but only to the extent that fluvial patterns allowed this to

happen in New Zealand's strongly east-west flowing river systems – unless the species are highly vagile and are able to move across inhospitable terrain to reach other hospitable areas. The extent of this happening, and its implications for the distribution and biogeography of the fauna, are unknown. Although most New Zealand rivers flow either eastwards (east of the mountain ranges) or westwards (west of the mountains), climatic gradients can be both east-west, in relation to altitude, and north-south in relation to latitude. Species' distributions are more likely to reflect altitude than latitude, following the east-west environmental gradients because of the predominant, east/west orientation of the rivers – though there was perhaps wandering in other directions between river catchments, across flood plains/extended coastal plains especially at times of lowered sea levels and especially across the Canterbury Plains. Less attention has been given to similar processes on the Southland Plains, in far southern New Zealand, but it is very likely that there, too, river systems wandering across alluvial surfaces, and shifting connections between various of the rivers, especially in the headwaters of rivers like the Maitai and Oreti, will have contributed to non-diadromous species being widespread and to a lack of genetic differentiation across river systems. Similar types of issues relate to all biotic elements, and Wardle (1991) has suggested that New Zealand plants have often failed to redispersed to occupy the full extent of their potential natural ranges across the landscape than might be indicated by their environmental tolerances. The same is almost certainly true for non-diadromous freshwater fishes, though it needs to be recognised that their ability to spread across the landscape amongst river catchments is constrained by their need for immersion in water.

References

- Adams J (1981) Earthquake-dammed lakes in New Zealand. *Geol Today* 9:215–219
- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Alloway B, Neall VE, Vucetich GG (1995) Late Quaternary (post 28, 000 years BP) tephrostratigraphy of northeast and central Taranaki, New Zealand. *J R Soc N Z* 25:385–458
- Andersen JC (1942) Maori place names – also personal names and names of colours, weapons and natural objects. Polynesian Society, Wellington, N Z, 494 pp
- Anon. (1942) Pioneer of acclimatisation activities: the story of Hatupatu. *N Z Outdoor* 4(11):27–29
- Baker A (1991) A review of New Zealand ornithology. In: Power D (ed) *Current ornithology*. Lenu, New York, NY, pp 1–67
- Barker JR, Lambert DM (1988) A genetic analysis of populations of *Galaxias maculatus* from the Bay of Plenty: implications for natal river return. *N Z J Mar Freshwater Res* 22:321–326
- Berrebi P, Cattano-Berrebi G, Valade P, Ricou J-F, Hoareau T (2005) Genetic homogeneity in eight freshwater populations of *Sicyopterus lagocephalus*, an amphidromous gobiid of La Réunion Island. *Mar Biol* 148:179–188
- Best E (1929) Fishing methods and devices of the Maori. *Bull Dom Mus* 12:1–230
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries and internal structure. *Ann Rev Ecol Syst* 27:597–623
- Brown JR, Beckenback AT, Smith MJ (1993) Intraspecific DNA sequence variation of the mitochondrial control region of white sturgeon, *Acipenser transmontanus*. *Mol Biol Evol* 10:326–341

- Burridge CP, Craw D, Waters JM (2006) River capture, range expansion, and cladogenesis: the genetic signature of freshwater vicariance. *Evolution* 60:1038–1049
- Closs GP, Smith M, Barry B, Markwitz A (2003) Non-diadromous recruitment in coastal populations of common bully (*Gobiomorphus cotidianus*). *N Z J Mar Freshwater Res* 37:301–310
- Cromarty P, Scott DA (1996) A directory of wetlands in New Zealand. Department of Conservation, Wellington, N Z, 395 pp
- Crosby R (2004) Gilbert Mair: Te Kooti's nemesis. Reed, Auckland, N Z, 352 pp
- Darlington PJ (1957) Zoogeography: the geographical distribution of animals. Wiley, New York, 675 pp
- Davey M, O'Brien L, Ling N, Gleeson DM (2003) Population genetic structure of the Canterbury mudfish (*Neochanna burrowsius*): biogeography and conservation implications. *N Z J Mar Freshwater Res* 37:14–22
- David B, Chadderton L, Closs G, Barry B, Markwitz A (2004) Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*). *DOC Sci Int Ser* 160:1–23
- Dijkstra LH (1999) The question of stocks and the whitebait fishery. *Cons Sci Newslett* 32:8
- Dijkstra LH, Jellyman DJ (1999) Is the subspecies classification of the freshwater eels *Anguilla australis australis* Richardson and *A. australis schmidtii* Phillipps still valid? *Mar Freshwater Res* 50:261–263
- Douglas BJ (1986) Lignite resources of Central Otago: Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessments and exploration models. *N Z Energy Res Devel Comm Publ* 104:1–368
- Fitzharris BB, Mansergh DG, Soons JM (1992) Basins and lowlands of the South Island. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 407–423
- Fletcher HJ (1919) The edible fish of Taupo-nui-a-tia. *Trans Proc N Z Inst* 51:259–264
- Gaston KJ (1990) Patterns in the geographical ranges of species. *Biol Rev* 65:105–129
- Gaston KJ (2003a) The structure and dynamics of geographic ranges. Oxford University Press, Oxford, 280 pp
- Gaston KJ (2003b) The how and why of biodiversity. *Nature* 421:900–901
- Greve M, Gremmen NJM, Gaston KJ, Chown SL (2005) Nestedness of Southern Ocean island biotas: ecological perspectives on a geographical conundrum. *J Biogeogr* 32:155–168
- Griffin LT (1936) Revision of the eels of New Zealand. *Trans Proc R Soc N Z* 66:12–26
- Gyllenstein U (1985) The genetic structure of fish: differences in the intraspecific distribution of biochemical variation between marine, anadromous and freshwater species. *J Fish Biol* 26:691–699
- Hicks AS, David BO, Swearer S, Closs GP (2008) Lake health and non-diadromous recruitment is crucial for banded kokopu in the Waikato River system. In: Back to science: the importance of freshwater science to freshwater management: New Zealand Freshwater Sciences Society, 24–27 November 2008, New Plymouth, Abstracts, unpaginated
- Hoareau T, Bosc P, Valade P, Berrebi P (2006) Gene flow and genetic structure in *Sicyopterus lagocephalus* in the south-western Indian Ocean, assessed by intron-length polymorphism. *Exper Mar Biol* 349:223–234
- Humphries CJ (2004) From dispersal to geographic congruence: comments on cladistic biogeography in the twentieth century. In: Williams DM, Forey PL (eds) Milestones in systematics. Systematics Association Special Volume Series 67. CRC Press, Boca Raton, FL, pp 225–260
- Irwin J (1975) Checklist of New Zealand lakes. *N Z Oceanogr Inst Mem* 74:1–160
- Keith P, Galewski T, Cattaneo-Berrebi G, Hoareau T, Berrebi P (2005) Ubiquity of *Sicyopterus lagocephalus* (Teleostei: Gobioidae) and phylogeography of the genus *Sicyopterus* in the Indo-Pacific area inferred from mitochondrial cytochrome b gene. *Mol Phyl Evol* 37:721–732
- King KJ, Young KD, Waters JM, Wallis GP (2003) Preliminary genetic analyses of koaro (*Galaxias brevipinnis*) in New Zealand lakes: evidence for allopatric differentiation among lakes but little population subdivision within lakes. *J R S N Z* 33:591–600
- Lee DE, McDowall RM, Lindqvist JK (2007) *Galaxias* fossils from Miocene lake deposits, Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *J R Soc N Z* 37:109–130

- Ling N, Gleeson DM, Willis KJ, Binzegger SU (2001) Creating and destroying species; the 'new' biodiversity and evolutionary significant units among New Zealand's galaxiid fishes. *J Fish Biol* 59(Suppl A):209–222
- Lowe DJ, Green JD (1987) Origins and development of the lakes. In: Viner A (ed) *Inland waters of New Zealand*. Department of Scientific and Industrial Research, Wellington, N Z, pp 1–64
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 107–143
- Lucas MC, Baras E (2001) *Migration of freshwater fish*. Blackwell Science, Oxford, 420 pp
- Maes GE, Volckaert FAM (2002) Clinal genetic variation and isolation by distance in the European eel *Anguilla anguilla* (L.). *Biol J Linn Soc* 77:509–521
- Main MR (1989) Distribution and post-glacial dispersal of freshwater fishes in South Westland, New Zealand. *J R Soc N Z* 19:161–169
- Mayr E (1963) *Animal species and evolution*. Belknap, Cambridge, MA, 797 pp
- Mayr E, Diamond J (2001) *The birds of northern Melanesia*. Oxford University Press, Oxford, 492 pp
- McDowall RM (1967) New landlocked fish species of the genus *Galaxias* from North Auckland, New Zealand. *Breviora* 265:1–11
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1976) Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J R Soc N Z* 6:17–22
- McDowall RM (1979) Fishes of the family Retropinnidae (Pisces: Salmoniformes) – a taxonomic revision and synopsis. *J R Soc N Z* 9:85–121
- McDowall RM (1984) *The New Zealand whitebait book*. Reed, Wellington, N Z, 210 pp
- McDowall RM (1990) *New Zealand freshwater fishes: a natural history and guide*. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1994) The Tarnsdale bully, *Gobiomorphus alpinus* (Pisces: Eleotridae) revisited and redescribed. *J R Soc N Z* 24:117–124
- McDowall RM (1996a) Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Can J Fish Aquat Sci* 53(Suppl 1):219–236
- McDowall RM (1996b) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1997) Affinities, generic classification, and biogeography of the Australian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Rec Aust Mus* 49:121–137
- McDowall RM (1998) Driven by diadromy: its role in the historical and ecological biogeography of New Zealand freshwater fishes. *Ital J Zool* 65(Suppl S):73–85
- McDowall RM (2000) *Reed field guide to New Zealand freshwater fishes*. Reed, Auckland, N Z, 224 pp
- McDowall RM (2001) Anadromy and homing: two life history traits with adaptive synergies in salmonid fishes? *Fish Fish* 2:78–85
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McDowall RM (in press) *Ikawai: freshwater fish in Maori culture and economy*. Canterbury University Press, Christchurch, N Z
- McDowall RM, Frankenberg RS (1981) The galaxiid fishes of Australia. *Records of the Australian Museum* 33:443–605
- McDowall RM, Lee DE (2005) Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *J R Soc N Z* 35:339–344
- McDowall RM, Pole M (1997) A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J R Soc N Z* 27:193–198
- McDowall RM, Stevens MA (2007) Taxonomic status of the Tarnsdale bully *Gobiomorphus alpinus* (Teleostei: Eleotridae), revisited – again. *J R Soc N Z* 37:15–29
- McDowall RM, Kennedy EM, Alloway BV (2006a) A fossil southern grayling, genus *Prototroctes* (Teleostei: Retropinnidae) from the Pliocene of northeastern New Zealand. *J R Soc N Z* 36:27–36

- McDowall RM, Kennedy EM, Lindqvist JK, Lee DE, Alloway BV, Gregory MR (2006b) Probable *Gobiomorphus* fossils from the Miocene and Pleistocene of New Zealand (Teleostei: Eleotridae). *J R Soc N Z* 36:97–109
- Milner AM (1987) Colonization and ecological development of new streams in Glacier Bay National Park. *Freshwater Biol* 18:53–70
- Milner AM, Bailey RG (1989) Colonization of new streams in Glacier Bay National Park, Alaska. *Aqua Fisheries Man* 10:179–192
- Neall V (1992) Landforms of Taranaki and the Wanganui lowlands. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 287–307
- Northcote TG, Ward FJ (1985) Lake resident and migratory smelt *Retropinna retropinna* (Richardson), of the lower Waikato River system. *N Z J Mar Freshwater Res* 17:113–129
- Northcote TG, Hendy CH, Nelson CS, Boubée JAT (1992) Tests for migratory history of the New Zealand common smelt (*Retropinna retropinna* (Richardson)) using oxygen isotopic composition. *Ecol Freshwater Fish* 1:61–72
- Ovenden JR, White RWG (1990) Mitochondrial and allozyme genetics of incipient speciation in a landlocked population of *Galaxias truttaceus* (Pisces: Galaxiidae). *Genetics* 124:701–716
- Raadik T (2001) When is a mountain galaxias not a mountain galaxias. *Fish Sahul* 15:785–789
- Reed AW (1952) The story of New Zealand placenames. Reed, Wellington, N Z, 143 pp
- Schmidt J (1928) The fresh-water eels of New Zealand. *Trans Proc N Z Inst* 58:379–388
- Smith PJ, Benson P, Stanger C, Chisnall BL, Jellyman DJ (2001) Genetic structure of New Zealand eels *Anguilla dieffenbachii* and *A. australis*. *Ecol Freshwater Fish* 10:132–137
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tarndale bully revisited with molecular markers: an ecophenotype of the common bully *Gobiomorphus cotidianus* (Pisces: Gobiidae). *J R Soc N Z* 33:663–673
- Smith PJ, McVeagh SM, Allibone RM (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Stafford DM (1967) Te Arawa: a history of the Arawa people. Wellington, Reed, N Z, 573 pp
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Taiaroa-Smithies K, Taiaroa M (2006) Legends of Ngatoro-i-rangi. Reed, Auckland, N Z, 72 pp
- Tapsell E (1972) A history of Rotorua: a brief survey of the settlement of Rotorua and environs by our pioneers. Maori and Pakeha, Hutcheson, Bowman and Stewart, Wellington, N Z, 152 pp
- Wallis GP, Judge KF, Bland J, Waters JM, Berra TM (2001) Genetic diversity in New Zealand *Galaxias vulgaris* sensu lato (Teleostei: Osmeriformes: Galaxiidae): a test of a biogeographic hypothesis. *J Biogeogr* 28:59–67
- Ward RD, Woodward M, Skibinski DOF (1994) A comparison of diversity levels in marine, freshwater, and anadromous fishes. *J Fish Biol* 44:213–232
- Wardle P (1991) Vegetation of New Zealand. Cambridge University Press, Cambridge, 672 pp
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, White RWG (1997) Molecular phylogeny and biogeography of the Tasmanian and New Zealand mudfishes (Salmoniformes: Galaxiidae). *Aust J Zool* 45:39–48
- Waters JM, Wallis GP (2001) Cladogenesis and loss of the marine life history phase in freshwater galaxiid fish (Osmeriformes: Galaxiidae). *Evol* 55:587–597
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid fish lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Waters JM, Dijkstra LH, Wallis GP (2000) Biogeography of a Southern Hemisphere freshwater fish: how important is marine dispersal. *Mol Ecol* 9:1815–1821
- Waters JM, Craw D, Youngson JH, Wallis GP (2001) Genes meet geology: fish phylogeographic pattern reflects ancient rather than modern drainage patterns. *Evolution* 55:1844–1855
- Waters JM, Rowe DL, Burridge CP, Wallis GP (in press) Gene trees versus species trees: reassessing life history evolution in a freshwater fish radiation. *Syst Zool*

- Young KD (2002) Life history of fluvial and lacustrine landlocked koaro (*Galaxias brevipinnis*) Günther (Pisces: Galaxiidae) in the Tarawera lakes. Unpublished MSc thesis, University of Waikato, Hamilton, N Z, 84 pp
- Zattara EE, Premoli AC (2005) Genetic structuring in Andean landlocked populations of *Galaxias maculatus*: effects of biogeographic history. *J Biogeogr* 32:5–14
- Zink RM, Fitzsimons JM, Dittman DL, Reynolds DR, Nishimoto RT (1996) Evolutionary genetics of Hawaiian freshwater fish. *Copeia* 1996:330–335

Chapter 19

Some General Biogeographical Patterns in the Fish Fauna

Abstract Distribution patterns are the product of processes, including the arrival of taxa from other lands across the seas around New Zealand, localised speciation, dispersal of diadromous species through coastal seas, and historical geological processes that have affected New Zealand, mostly since its emergence from extensive marine submergence in the Oligocene. Distribution patterns to some extent mirror patterns in other taxonomic groups, though many of the patterns are idiosyncratic for freshwater fishes, owing to their distinctive restriction to aquatic habitats as well as the ability of diadromous freshwater species to spread around the Southern Ocean through the sea. The uplift of the Southern Alps, substantially coincidental with climatic cooling that took place from late Miocene times until the Pleistocene, resulted in the evolution of an alpine biota, and this included fish species that are largely found in the streams of the intermontane valleys of the mountains.

Keywords Alpine biota • Climate change • Congruence • Diadromy • Dispersal • Earth history • Mountain building • *Nothofagus* • *Paranephrops* • Pteridophytes • Speciation

19.1 Understanding Pattern and Process

Understanding pattern and process in the biogeography of New Zealand freshwater fishes is, perhaps, somewhat hindered by the lack of strongly established phylogenetic hypotheses for the various families and genera, though the various species groups discussed above are now well-enough established to permit a search for synthesis, and this is the purpose of the present section. I will attempt to do this at a series of spatial and temporal scales. Insofar as we are looking at patterns in the fauna of a discrete biogeographical area, an area that has a single, overall, geological and climatological history, it can perhaps be expected that aspects of species' distributions affected by geology/history, will exhibit commonalities – although interspecific ecological/behavioural/life history variation may mean that there will be different responses to various influences across the species groups.

Looming in the background to all these phylogenetic and ecological scenarios is the history of the New Zealand landscape discussed in earlier chapters, with New Zealand's ancient-to-recent geological and climatic events and processes:

- The late Mesozoic origins of Zealandia in Gondwana
- Early Cenozoic submergence beneath the sea – partial, extensive, or even total
- The implications of major topographical changes and connections as a result of movements associated with the Alpine Fault
- Major climate changes including the Pleistocene glaciation, that were happening until recent times and are still occurring
- Enduring, active volcanism over a long period and widely across the country these being of varying importance in causing biotic patterns and thus in providing explanations for them.

Specifically, several contributing, alternative questions arise:

- To what extent does the evidence support past assertions that dispersal has been pivotal in establishing distributions (McDowall 1964, 1978, 1990, 2002; McDowall and Whitaker 1975)?
- To what extent does the evidence support the ideas of Rosen (1974) Croizat et al. (1974), Campos 1984), Craw (1979, 1989) and others, who argue that we are looking primarily at the influences of ancient vicariance processes associated with Gondwana, and thus with the changing global geography?
- Do both of these scenarios apply, since they need not be viewed as true alternatives (i.e. are they mutually exclusive possibilities) – is it a question of dispersal biogeography superimposed on the geological history of Zealandia?

Furthermore:

- Is there general evidence, for instance, that supports the statement of Croizat (1952, 1958, 1964; Craw et al. 1998, Ebach et al. 2003; Humphries 2004) that earth and life evolved together?
- Is Knapp's (2005) statement that the "dictum that earth and life evolve together is self-evident and true across all time scales" really true, does it have only limited application, or is it mere assertion?
- Or, more generally, is there any basis for the assertion of Heads and Patrick (2003) that species "stay put"?

Page (1989), Grehan (1989) and Craw (1989) all concurred with Croizat (1952) in questioning the 'conventional wisdom' that the distribution patterns of species with greatly differing ecologies are different, and argued for taxa with different ecologies having similar distributions. However, this 'conventional wisdom' is plainly applicable to the distributions of New Zealand's freshwater fishes, where behavioural ecology mediates fundamentally different distribution patterns that relate to whether species are diadromous, or not. There are very clearly deep, and fundamental, differences in the distributions and biogeographies of diadromous and non-diadromous species across the families in the fauna, based substantially around ecology.

There are some points of similarity across the biogeographies of non-diadromous species groups that tend to relate to the more obvious, potential major historical influences on distribution patterns, such as the presence or absence of marine straits between the major islands, the impacts of Recent volcanism in the central North Island, or uplift of the Southern Alps. Distinct differences emerge, however, when an attempt is made to fit the various individual species-group scenarios together both spatially and temporally. Each species group seems to have its own patterns of presence/absence, areas of diversification, and sometimes there is very poor congruence in distribution patterns between groups. We seem, then, to be looking at a paradox that, at least for non-diadromous species, “earth and life [appear to] evolve together” (Croizat 1952, 1958, 1964; Humphries 2004; Knapp 2005) at the within-species-complex scale for non-diadromous species, but at a breakdown of this mantra when distributions are compared across non-diadromous species complexes (as well as being universally untrue for the diadromous species). Thus the conclusion that “earth and life evolve together” though sometimes true at the within-group scale, seems essentially untrue at the among-group scale, and is therefore essentially trivial in a broad, synthetic, historical biogeographic context.

Mayden (1988) found that in an area of North America “the pattern of relationships between fish occurring in different river basins better reflects past drainage patterns than drainage patterns we see today”. This is, however, in general, untrue for New Zealand’s non-diadromous fish species – the distributions of the various species groups seem to conform to the widely existing, contemporary patterns of river drainages and connections – though there are a few interesting and clearly identified instances in which distributions of non-diadromous species are associated more with explicitly known historical changes in the directions of rivers than contemporary ones (such as is observed in the Von and Nevis Rivers in Central Otago, and perhaps in relation to the Lewis Pass and old fluvial connections there between the Buller River to the west and the Waiau River to the east: McDowall 1970; Waters et al. 2001; Smith et al. 2003; BurrIDGE et al. 2006); Tarndale bully in the lakes at the head of the Wairau and Clarence Rivers (McDowall and Stevens 2007); or dwarf galaxias in relation to the Pelorus and Wairau River drainages in northern Marlborough (Craw et al. 2007).

As other geological and molecular information emerges, additional biotic connections may be recognised; or, alternatively, knowledge of biotic distributions could be the drivers of searches for additional catchment flow direction changes. And, there are a number of scenarios in which lineage distribution patterns have what might seem to be ad hoc congruence’s with diverse geological events/patterns. We can look forward to further reciprocal illumination of history and ecology, and though in essence we need to interpret biogeographical patterns in the context of geological history (McDowall 1973), there are probably also instances when knowledge of biotic distributions may highlight areas of geological interest (McDowall 2008).

Some evolutionary biologists tend to the view that a group’s centre of diversity is its centre of origin, but why this should be so is not intuitively obvious. Centres of origins, if one believes in them (and some apparently don’t – Croizat et al. 1974), seem more likely to be in areas where there have been opportunities to enter different

adaptive zones and/or, at least in freshwater fishes, there has been re-arrangement of fluvial connections that facilitate establishment of barriers to gene flow, and there seems no fundamental reason that this should be predominantly in any area of a taxon's range, whether at the centre, around the periphery, or at the extreme margins. Mayr (1982; Mayr and Diamond 2001), rather than a centre of origin, referred to the importance of "peripatric speciation", in which speciation is present in local isolates around the fringes of a species range, and these fringe locations may be either geographically or ecologically 'fringe' locations. There seems no compelling reason to assume that the centre of diversity of pencil-galaxias in the Mackenzie Basin relates to that area being a centre of origin for the complex as a whole, but it could be. The Mackenzie Basin could perhaps be a rather recent area of speciation/diversification, especially given the likelihood of major disruption by glaciation, though there is also a prospect that the land surface of the basin may once have been associated with hypothesised enduring southern island during the Oligocene drowning of New Zealand (Cooper and Cooper 1995) (see Fig. 3.2).

Zemlak et al. (2008) have pointed to an important role for mountain-building in the Andean Mountains of Patagonian South America in leading to separation of stocks in the non-diadromous species *Galaxias platei*. They estimate (p. 5057) that the Andes have "separated *Gl. platei* into eastern and western lineages for at least 1.5 Ma", as well as finding deep genetic structure within each of the western and eastern lineages. Somewhat similar scenarios are evident in eastern and western stocks of New Zealand's upland bully, where Smith et al. (2005) demonstrate deep divergence to the extent that distinct taxa may be represented in the eastern and western lineages. At a more local geographic scale, deep divergence has been identified among the two species of longjaw galaxias, estimated on the basis of differences in molecular sequencing, as dating back to late Miocene or Pliocene times (McDowall and Waters 2002). Much, therefore, remains to be learned about the interactions of geological and climatic history, patterns of river catchment connections and separations, and the patterns of species' distributions and taxonomic diversity in the New Zealand freshwater fish fauna. Zemlak et al. (2008: 5058) observed "further subdivision" of the lineages on both eastern and western sides of the Andes, where catchments on each side of the Andes were subdivided into separate glacial refuges as a result of repeated Pleistocene glacial cycles; hitherto, nothing comparable with this has been identified in New Zealand, perhaps because the scale of the New Zealand landscape is so much smaller than in Patagonia. Perhaps, also, the situation is a little different in *Gl. platei*, which customarily inhabits large lakes (of which there are many in Patagonia), whereas there are no geographically widespread lacustrine galaxiids in New Zealand (owing, substantially, to the relative youth of most New Zealand lakes). And though Zemlak et al. (2008) suggest that the phylogeographic evidence supports the "original conclusions of McDowall (1971)" that "*Gl. platei* constituted one species over its entire range", they were clearly uncertain, and proposed further work to test the species-level status of *Gl. platei*. Given the age and spatial scale of the South American landscape and the levels of genetic diversity Zemlak et al. found, and recognising increased taxonomic diversity that has been discovered in recent years in both New Zealand (compare the 13 galaxiids

recognised in McDowall 1970 with the 20 species in McDowall 2000) and in Australia (where recognition of several additional species has been signalled by Raadik 2001, 2005), I have little doubt that what is at present regarded as the single species *Gl. platei* in South America (McDowall 1971) will be shown to represent greater taxonomic diversity than that.

19.2 Freshwater Fish Distributions in the Context of the Broader New Zealand Biota

New Zealand's Cenozoic-long geographical isolation in the south-western Pacific Ocean, and its lively geological turbulence during that long isolation, seem likely to have been among the most significant influences on patterns of evolution, speciation and distribution of the New Zealand fauna and flora (Gibbs 2006, McDowall 2008; Wallis and Trewick 2009), its freshwater fishes included. Wallis and Trewick (2009: 3548) wrote of "east-west splits across the Southern Alps, east-west splits across North Island, north-south splits across South Island", and no doubt these can be identified in the freshwater fish fauna. McGlone (1985) reckoned that active tectonism since the late Oligocene has been the main driver for many endemic, vicariant and disjunct plant distributions; and while the more stable geographical areas have developed, or retained, these individual, variously endemic floras, uplifting, unstable areas may not have done so, in part owing to the effects of increased elevation on ambient temperatures. New Zealand must therefore be viewed as having been geologically unstable and dynamic throughout the Cenozoic to Recent. To these physical geological changes must be added major global climatic variability from warm subtropical to cold glacial over a long time scale (Lee et al. 2001; Gibbs 2006; Campbell and Hutching 2007). However, the more recent major changes in and influences of all these factors are likely to have obscured or obliterated the impacts of earlier changes, i.e., recent events are likely to have 'overwritten' earlier ones (Waters and Craw 2006). Contemporary distribution patterns are likely to reveal mostly the impacts of the most recent, substantial events, whether physical or climatic.

Pole (1994) postulated that the influences of Oligocene submergence on New Zealand, its geology, and climate, were so massive that the flora we observe today is derived entirely by dispersal from outside the New Zealand region since that submergence – the implication being that all of the existing landscape was submerged. Later, however (Pole 2001), he rather 'softened' his position and accepted that submergence may not have been complete, and some ongoing work is supporting this (Stockler et al. 2002; Lee et al. 2008). However, Campbell and Landis (2001, 2005), Campbell and Hutching (2007), and Landis et al. (2008) persist with the prospect of complete submergence. Waters and Craw (2006) concluded that there is "no direct evidence" for continuously emergent land anywhere in New Zealand through the middle Cenozoic (e.g. as signified by a continuous sequence of non-marine sediments from Eocene to Miocene), and they suggest that

there is therefore no sound geological basis for the proposed shape/size/position of proposed islands emergent though the Oligocene of Fleming (1979), at which time everyone agrees that there was certainly very substantial submergence of areas that are now emergent land (Cooper and Cooper 1995; Cooper 1998). Waters and Craw (2006) inclined to the view that the residual, small islands suggested by Fleming were a response to hypothesised biological/biogeographical needs rather than to well-formed geological hypotheses – an argument vulnerable to circularity. There is, however, phylogeographical evidence, based on dates from molecular sequences, which suggests that at least some plant groups may have survived in New Zealand from Gondwanan times to the present (such as the tree genus *Agathis* – Stockler et al. 2002; Lee et al. 2008), though Waters and Craw (2006) suggest that it is premature to reject post-Oligocene arrival of *Agathis* in New Zealand. It seems intuitively likely that other biotic elements, such as the tuatara, hyridellid freshwater mussels, parastacid freshwater crayfishes and their temnocephalid commensals (McDowall 2005a), leiopelmid frogs, perhaps peripatus, some argue for some of New Zealand's ratite birds, and no doubt other groups, have an ancient and continuous presence that may reflect New Zealand's former Gondwana connection (Daugherty et al. 1993; Winkworth et al. 2005). Phreatoicid amphipods are another possibility (Wilson 2008). Jones et al. (2008) have recently reported tuatara fossils from the Early Miocene of Central Otago (19–16 million years ago), adding to a rich biota of that area that seems likely to have been present there for a substantial period – or major dispersal events covering a wide range of taxa are needed to explain what has been reported from that area. Boyer and Giribet (2009) have recently argued for a group of opiliones (Arachnida), the Pettalidae, to be an ancient Gondwanan element in New Zealand, with three different, monophyletic species groups in New Zealand, each with external relationships in Australia, in their view supporting a claim for an ancient, Gondwanan ancestry/distribution. The alternative is three separate dispersal events in a group they consider unlikely to do so. Others, too, are suggesting a continuous land surface somewhere in New Zealand, recent among them being Worthy et al. (2009) and Wallis and Trewick (2009). I discussed earlier the suggestion that the acanthisittid wrens of New Zealand are ancient relics (Ericson et al. 2002), and that Worthy et al. (2009), finding a diverse, distinctly New Zealand fauna in the early Miocene, suggest that this fauna, including a small mammal and tuatara (*Sphenodon*) must have been of some age, again suggesting land somewhere in the Oligocene. There could have been rapid radiation to produce a distinctively New Zealand biota, but this is of little help in explaining the presence of very basal taxa like the wrens, or an ancient taxon like the tuatara.

It is interesting that as long ago as 1896, New Zealand biologist/geologist F.W. Hutton was exploring these same issues, not in the explicit context of Gondwana and plate tectonics, but very much with the prospect of New Zealand's association, together with other lands, as part of what he referred to as “the theory of the former existence of a South Pacific Mesozoic continent”, which Hutton thought was the “only theory left”, after exploring a series of options to explain the biogeographical relationships of the New Zealand flora and fauna. Moreover, it is interesting that he, too, alluded to the biogeographical difficulties created by the presence in New Zealand of “*Sphenodon*,

Unio [now known as *Echyridella*, the freshwater mussel] and *Astacidae* [now known as *Paranephrops* the koura or freshwater crayfish], none of which are found in truly Oceanic islands...New Zealand must have formed part of a large island joined to New Caledonia, but not to Australia....Still later, again, New Zealand must have stretched south and obtained its Antarctic fauna and flora from Patagonia through a number of islands" (Hutton 1896); thus he was wrestling, then, with problems that continue to create discussion and controversy over a century later.

Gibbs (2006) nominated the endemic scorpionfly *Nannochorista philpotti* and the kauri tree, *Agathis australis* as "emblems" of former, ancient land connections. But it is possible that kiwis and perhaps even moas flew to New Zealand more recently than the late Cretaceous detachment of Zealandia (proto-New Zealand) from Gondwana (Cooper et al. 2001; Haddrath and Baker 2001; Waters and Craw 2006; Gibbs 2006; Harshman et al. 2008). However, even though observed lineage connections between extant New Zealand taxa and others elsewhere appear to be ancient, we cannot exclude the possibility that lineage extinctions elsewhere are obscuring more recent connections that would require dispersal events. And *Nannochorista* has a flighted adult and so may have an ability to disperse that might not be expected if it was restricted to freshwater habitats.

Even though there may not have been the complete replacement of the fauna, that Pole's (1994) dispersal-origin hypothesis for the New Zealand flora postulated, it seems likely that there were repeated, very major, restructurings of the New Zealand biota through the Cenozoic, provoked by:

- The Oligocene submergence, just discussed and, at the very least, major reduction and fragmentation of the emergent New Zealand land mass.
- Major climate change, with cooling of temperatures dating from the Miocene, which is interpreted as causing major losses to the New Zealand flora of warmth-loving plant elements often with Australian and New Caledonian relationships (Lee et al. 2001), and also including Pleistocene glaciation, and perhaps this recent climatic change is the most easily seen.
- Massive, enduring and widespread volcanism, some of it very recent.

Campbell and colleagues (Campbell 1998; Campbell and Trewick 2003; Campbell and Hutching 2007; Campbell et al. 2009) have been exploring the likely prospect (from geological evidence) that the Chatham Islands, ca. 800 km east of the main islands of New Zealand (see see Figs. 1.1, 2.1), and once part of Zealandia, may have been entirely submerged beneath the sea at some stage during the Cenozoic, and confirmation of such an event would have profound implications for understanding Chatham Islands biogeography across a wide range of plant and animal taxa, relative to that of mainland New Zealand (Emberson 1995; Trewick 2000). This includes the freshwater fishes there – though all but one of them are diadromous. The Chatham mudfish isn't, and nor is its closest sister species (Canterbury mudfish (McDowall 2004; Waters and McDowall 2005) – but perhaps the fact that all other species in the Chathams freshwater fish fauna are diadromous does tell us something about the islands' biogeography, about how freshwater fish reached them, and *Neochanna* does have a diadromous ancestry (McDowall 2004; Waters

and McDowall 2005). It could have dispersed there, through the sea, but this, of course, must have happened since the islands emerged from the sea perhaps as recently as a few million years ago (Campbell and Hutching 2007; Campbell et al. 2009). This seems to point to diadromy having been present in *Neochanna* rather more recently than we might have predicted, if we are to account for the Chatham mudfish (see Chapter 14), this species being close to basal in the New Zealand members of this small radiation involved (Waters and McDowall 2005).

There is no reason to think that New Zealand's freshwater fish fauna would have escaped the impacts all of this prolonged, Cenozoic to Recent geological turbulence and climatic instability that has been characteristic of the New Zealand landscape (McDowall 1996a, 1998, 2002) – even though the nature, intensity, and geography of the impacts in terrestrial and aquatic environments may have differed. Freshwater fish distribution patterns suggest that changes that influenced the biota as a whole did have impacts on freshwater fish, though these impact persist only with regard to the non-diadromous species, given the ability of diadromous fishes to sustain restoration (McDowall 1996b). Thus, to the extent that biotic distributions are influenced by New Zealand's geological and climatic history, it could be expected that there should be some similarities in distributions across different taxonomic groups. The biota, as Cracraft (1994) put it, might be expected to have a spatial history of areas of endemism “within which the assembly is embedded”.

There ought, however, also to have been some distinctive features in the biogeography of freshwater fish compared with other taxonomic groups, because river systems have very strong linear connectivity along their narrow channels, and this is accentuated by their directional upstream-downstream flows, but they have less spatial connectedness across other dimensions – rivers taken as a whole tend to be highly discrete and physically separated, especially in comparison to terrestrial habitats that are not so restrictive in broadening species' ranges. Nevertheless, I very much doubt that anything would, or could, have “stayed put” as suggested as a generality by Heads and Patrick (2003). The widespread presence of diadromy will have mitigated the separation of river systems by allowing dispersal between catchments through coastal seas at least for the diadromous fraction of the fauna.

As discussed in the previous chapter, New Zealand's rivers tend to be quite strongly aligned across the narrow east-west dimension of the archipelago and, to the extent that they are so aligned, they run parallel to altitudinal environmental gradients but are perpendicular to the axes of mountain ranges as well as to latitudinal gradients in such variables as temperature. This would have affected dispersal across the New Zealand landscape; much the greatest freshwater fish diversity is in the eastern/southern South Island, and this is perhaps enigmatic when the area is very much in the rain shadow of the Southern Alps, and so exhibits low rainfall, but perhaps this has resulted in more stable land- and river-scapes within which fish species can persist and diversify across geological time scales. Also, however, freshwater habitats are often small in area, and may be more ephemeral than terrestrial ones especially across these same geological time scales. New Zealand's lakes tend to be especially young, mostly post-Pleistocene in age (Lowe and Green 1987, 1992) – mostly an outcome of late Cenozoic to Recent glaciation and

volcanism. Overlying all of this, in the freshwater fish fauna, will be the distinctive impacts of diadromy, as it allows much wider dispersion to New Zealand from elsewhere and, once taxa are here, dispersion around New Zealand, and these diadromous species have historically provided the core material for the establishment of non-diadromous sister taxa and the evolution of greater taxonomic diversity.

There are some significant biogeographical similarities or contrasts between the terrestrial and freshwater biotas in New Zealand, and that should occasion no surprise. Similarities include the loss of biota from the central North Island volcanic zone (McDowall 1996b), just as in other taxa (Clarkson 1990; Clarkson et al. 1988). But, although Gibbs (2006) mentions “at least” 11 instances where the southern North Island constitutes a major gap in the distributions of taxa known from the northern North Island and the northern South Island, this is not true of any freshwater fish. As in the freshwater fishes, there are many biotic distributions of other groups that span Cook Strait and Foveaux Straits. Te Punga (1953) long ago drew attention to the fact that the distributions of many taxa, such as paryphantid snails (Gastropoda), involved land areas now separated by Cook Strait, and other workers have added additional taxa, (Hopkins 1970; Fleming 1979; Jamieson 1998) including koura or freshwater crayfish (Crustacea) (Fig. 19.1; McDowall 2005a). Lewis and Carter (1994), explicitly supported Te Punga’s (1953) hypothesis of a “periodically emergent land bridge that resulted in a complex speciation of the sedentary land fauna on either side of the ‘narrows’” (see Gibbs 2006). However, Brownsey (2001) recognised that Cook Strait was not influential as a barrier to north-south spread of ferns, at least partly owing to former land connections where there is now sea, though we cannot ignore the high likelihood of fern dispersal across the existing, narrow sea gap, and the capacity for dispersal, with their tiny, dust-like spores.

Biogeographers seem to have given much less attention to the effects on biotic distributions of known land connections across Foveaux Strait. This sea strait seems, however, to have little residual biogeographical impact. Non-diadromous freshwater fish like Gollum galaxias, *Galaxias* ‘southern’, and upland bully are present on both sides of the strait. Similarly, the southern koura crayfish, *Paranephrops zealandicus*, is also present in both Southland and Stewart Island (Fig. 19.1). Wardle (1991) describes the island as sharing much of its flora with the southern South Island. Chadderton et al. (2003) described the freshwater isopod *Austridotea lacustris* as widely present in the southern South Island, Stewart Island (and also on Campbell Island to the south and Pitt Island, in the Chathams to the far east). So, the southern South Island and Stewart Island share many biotic elements, almost as though they were not separated by a sea strait, and of course they weren’t, in the Pleistocene.

Buckley and Young (2008) examined the taxonomic status of water boatmen (Insecta: f. Corixidae), in rivers of the northern South Island, and on the basis of molecular evidence (mitochondrial DNA), conclude that what had hitherto been regarded as two species (Young 1962) should be treated as a single one, thus making taxonomic decisions in the reverse direction to what has applied to non-diadromous galaxiids in the South Island. Buckley and Young (2008: 56) do comment that four



Fig. 19.1 Distributions of the two New Zealand species of koura or freshwater crayfish: *Paranephrops planifrons*, to the north and west of the hatched line diagonally across the South Island, and *P. zealandicus* to the south and east of that line; the curved line across the North Island approximates the northern limits of the range of upland bully, *Gobiomorphus breviceps*

clades they identified provided “dates of divergence and phylogeographic patterns... similar to those for the galaxiid fish *Galaxias vulgaris*,” where Waters and Wallis (2001) identified separate clades in the Buller River to the west and other catchments in Marlborough to the east. They note, however, that, corixids being flighted insects, are “obviously more vagile than the fish”, and so better at dispersing across non-watered landscapes than galaxiid fishes, so that gene flow between populations is easier.

19.3 Development of an Alpine Biota and Areas of Endemism

Just as there are a few distinctly sub-montane freshwater fishes, such as the pencil galaxias species, various botanists and biogeographers have suggested that Pleistocene glaciation and the associated climatic changes have been major determinants of plant distribution patterns in New Zealand (Wardle 1963, 1978, 1988, 1991; Burrows 1965; McGlone 1985; Gibbs 2006). There are distinctively alpine

taxa like the kea (the world's only alpine parrot), montane insects like cicadas, butterflies, wetas (flightless orthopteran crickets), even montane reptiles like geckos and skinks, and others (Gibbs 2006; Hill et al. 2009) signifying repeated evolution of alpine animal taxa, just as has been much more widely discussed for plants. Today's alpine elements in the New Zealand biota would probably have evolved substantially during the late Cenozoic owing to the combined, simultaneous, effects of developing glaciation and uplift of the mountain ranges (Wardle 1963, 1978, 1988; Fleming 1979; McGlone 1985; Mark and Adams 1973; Trewick et al. 2000; McGlone et al. 2001; Winkworth et al. 2005), both of which will have affected climate at the local scale, especially at inland sites. The implications for the New Zealand biota of the cold temperatures of the Pleistocene have long been recognised (Rutland 1888; Thomson 1910), and were explored by du Reitz (1960) and Dumbleton (1967), the last of whom suggested that winter diapause (dormancy) in insects and winter deciduousness in some native New Zealand flowering plants may have been an adaptive response to lowered Pleistocene winter temperatures. Dumbleton (1967) endorsed Wardle's (1963) suggestion that the relatively low level of deciduousness in the New Zealand flora, compared with its much greater presence in the cool temperate zone of the Northern Hemisphere, might suggest that Pleistocene temperature minima in New Zealand were less extreme than in Europe and North America (or otherwise there would be more deciduous tree species in New Zealand), though this may, in part, have been due to New Zealand having long had an oceanic climatic regime, whereas that in Europe was more continental.

Several commentators (Cockayne 1917; Wardle 1991; McGlone 1985; Gibbs 2006) commented on low endemism in geologically youthful regions, like the central South Island, suggesting that there has not been time for endemic biotas to develop. This is untrue for freshwater fish as indicated by the distinctive diversity in the Mackenzie Basin of the pencil-galaxias complex, though there is no comparable observed diversity in other fish groups such as the *Gl. vulgaris* species complex or upland bully, in both of which there is just the single lineage in the Mackenzie Basin. Wardle (1978) suggested, also, that this area was characterised by Pleistocene extinction, thinking that "the present rarity or complete absence of many species of the forest and subalpine scrub from the "waist" of the South Island attests to harsh conditions along and adjacent to the Southern Alps during the Pleistocene". Again, the same cannot be said for freshwater fish. Trewick and Wallis (2001), moreover, have drawn attention to endemic lineages of weta (endemic flightless crickets) in the central South Island, including endemic taxa in the Mackenzie Basin, as is true of the pencil-galaxias species.

Fleming (1979) suggested that "the central 'waist' of the South Island between Canterbury and Westland, where glaciers extended to the lowlands and produced barrier aprons of outwash gravels, has gained many of its plants as sparse invasions from north and south" (citing Burrows 1969), and he thought that similar patterns could be seen in some cicadas (Insecta). There is absolutely no evidence for this in the fish faunas of western-flowing rivers but some evidence in the east, where there are non-diadromous fish faunas of some diversity, as described above, and including Canterbury galaxias, species of the pencil-galaxias complex, Canterbury mudfish

and upland bully widely across the Waitaki River system in all but Canterbury mudfish, including the submontane Mackenzie Basin.

The concept of extirpation of all life along the central West Coast of the South Island has its beginning and long history in botany (Cockayne 1926; Willett 1950; McGlone 1985; Wardle 1963, 1978, 1988, 1991; McGlone 1985; Lee et al. 2001; McGlone et al. 2001, 2003; Gibbs 2006), and was extended to non-diadromous freshwater fish by Main (1989), and further broadened to examine some patterns among insects (Leschen et al. 2008). The extent of extirpation during the last glaciation is debated. McGlone (1985) hypothesised that there were refuges along the Fiordland/South Westland coastline, where plant species could have survived during periods of severe glaciation, these becoming restricted to small patches that provided for rapid reinvasion once climate became warmer and Pleistocene glacial ice retreated – perhaps these are equivalent to the “interfluves” discussed by Soons (1992) and the “nunataks” of Heenan and Mitchell (2003).

This local survival may have been true, also, in the distribution of the freshwater crayfish *Paranephrops zealandicus* which, unlike fish, is found in pockets south of the beech gap (Mahitahi to Stafford Rivers – McDowall 2005a). However, Apte et al. (2007) demonstrated that the pattern is rather more complex than hitherto thought, and argued for different lineages north and south of the beech gap rather than the gap splitting a single lineage; populations south of the beech gap belong to a distinct, quite widespread, southern (undescribed) lineage, rather than to the lineage widely present north of the gap. Other taxonomic groups, such as insects are also implicated in the beech gap, as might be expected (Trewick and Wallis 2001). Leschen et al. (2008) examined molecular patterns in two fungus beetles, finding in both “patterns of population divergence corresponding to recent glacial cycles”, though the geographical responses of the two species differed: one of them remains excluded from the zone of the beech gap while the other has invaded it, and Leschen et al. linked this difference to differences in ecology and dispersal, and there is another lesson here for the panbiogeographers who disclaim any links between distribution and ecology.

Stevens and Hogg (2004) examined patterns in allozymes across the distributions of two species of corophiid (freshwater) amphipod; they found both absent across the entire West Coast south of about Cape Foulwind, and thought that their distributions “may provide support for the effects of Pleistocene climate conditions”; thus, if geo-climate is the cause of this absence, it applies across a substantially wider geography than is reported for other ‘beech gap’ influences. There has been little or no commentary on what the availability of such refuges may have meant for riverine biotas, but the impacts of Pleistocene ice sheets in the river valleys may have been even more substantial than for terrestrial biotas. Whereas some terrestrial biotic elements may have found refuges on exposed ridges and outcrops (McGlone 1985), riverine biotas would seem likely to have been more comprehensively eliminated by glacial ice deposits, i.e., the rivers and streams of the valley floors, where fish would be found, would have been very severely, perhaps maximally impacted by glaciation, by icing in the deep valleys and the locking up of precipitation as snow in the mountains. Thus, it seems, to me, unlikely that there would have been refuges comparable to these interfluves/nunataks that could have been available for riverine freshwater fishes (and other organisms living in flowing freshwaters).

Fleming (1979) also discussed the presence of an endemic biota on Banks Peninsula that he thought might be derived from the peninsula's earlier status as an offshore island, and he recognised the same for the Poor Knights and Three Kings Island groups in northern New Zealand. Again, there is no hint of this for freshwater fish on any of these islands, or former islands, mainly, perhaps, because freshwater stream habitats on such small islands are limited, probably are ephemeral over geological time scales, and the fish faunas are dominated by diadromous species.

Thus, generalising, despite Heads and Patrick's (2003) assertion that species tend to "stay put", the history of the New Zealand biota has obviously been characterised by continual cycles of invasion from outside, and local extirpation, speciation and redispersal, as:

- (i) Land areas became submerged by seas, and re-emerged as dry land.
- (ii) Mountains rose and were eroded and alluvial plains developed where there was formerly sea.
- (iii) Coastlines extended and retreated in relation to sea level fluctuations.
- (iv) Connections between river systems changed.
- (v) Climate oscillated between colder and warmer, and many times.
- (vi) The landscape was influenced by recurring volcanism in many areas.
- (vii) Associated biotas on which species depended ecologically, came and went.
- (viii) Novel elements in the fauna arrived from elsewhere and other elements long in the biota became locally extirpated or even globally extinct.
- (ix) There was speciation and diversification.
- (x) Ordinary random dispersal processes affected biotic distributions.

The biotic patterns that we now observe as appearing more or less static are thus the outcome of all these dynamic processes over the epochs and millennia, and what we see today has probably been driven mostly by recent events. The enriching goal of biogeographical research is to seek to understand how the continually changing nature of the landmass/landscape, and of the climate, have affected the distributions of the various elements in the biota. And, whereas panbiogeographers like Craw (1979, 1989), Grehan (1989), Heads (1998), Craw et al. (1998), Heads and Patrick (2003), and others find their fulfilment in a search for explanations of a stationary biota 'frozen' in a stable landscape, over long geological epochs, others like McGlone (1985), Wardle (1963, 1978, 1988, 1991), Brownsey (2001), Wallis and Treweek (2001, 2009), Lee et al. (2001), Gibbs (2006), and me (McDowall 1964, 1978, 2002, 2008) have sought to determine the extent to which explanations of patterns rest in understanding arrival, establishment, dispersal, speciation, and extinction, on this dynamic, continually-changing, landscape and climate.

19.4 Comparisons of Patterns with Other Aquatic Biota

The distributions of aquatic invertebrates, which share ecosystems/habitats with freshwater fish, may provide mutual illumination of causal patterns. The only macro-invertebrates found in New Zealand fresh waters are two described species

of parastacid crayfishes, or koura (and there are probably additional undescribed species – Apte et al. 2007), an atyid shrimp, and hyridellid mussels. The shrimp is diadromous (Carpenter 1982), and it is perhaps interesting that there is just a single species with no taxonomic diversification – something that would be impeded by diadromy and associated, consequential coastal dispersal. And so its pattern of distribution and other aspects of its biogeography are likely to conform to the pattern of diadromous fish species, being widespread, revealing no connection to geological history (Cook and Crisp 2005), and having downstream-upstream gradients of abundance and population size structures similar to those found in diadromous fishes – there is likely to be absence upstream of barriers to migration, though this question has not been explored for the shrimp.

New Zealand's freshwater *Paranephrops* crayfishes, as well as their temnocephalid commensals are probably ancient (Crandall et al. 1999; Crandall 2000; Hansen and Richardson 2006), and possibly Gondwanan relicts (McDowall 2005a; Gibbs 2006; Apte et al. 2007). The biogeography of the species of koura is as idiosyncratic as that of various of the groups of non-diadromous freshwater fishes, but there are several aspects of pattern that are pertinent to a New Zealand freshwater fish biogeography.

The two koura species are separated by the mountain ranges of the South Island (Fig. 19.1), though whether this is a vicariance event, or is a result of some more ancient geological processes is unclear, and needs to be explored by further genetic sequencing studies (McDowall 2005a; Apte et al. 2007). There are two known instances where koura has a broader distribution in relation to perturbation (Mount Taranaki volcanic activity and the effects of West Coast Pleistocene glaciation) than some non-diadromous fishes, but where it shares its range with brown mudfish. Eldon (1968) reported brown mudfish and koura to occupy similar habitats and, as discussed earlier, is it possible that the wetland pockets, where both brown mudfish and koura are found, may be less influenced by perturbations in fluvial habitats? Apte et al. (2007), however, have shown the taxonomy of the stocks of *Paranephrops* to be rather more complex than the long-accepted scenario of two distinctly allopatric species (Hopkins 1970; McDowall 2005a), and further details of the group's biogeography must await further taxonomic study.

There is an interesting co-occurrence of the northern koura species and northern flathead galaxias in a headwater tributary of the Motueka River (see Fig. 11.2, arrow 1), and this is an instance of overlap of taxa with northern (koura) and southern (galaxiid) provenances. As well, both dwarf galaxias and upland bully are widespread across this area, so again we are looking at some individualistic dispersal processes.

Interestingly, koura, and also Cran's bully and upland bully create another interestingly complex nexus between stocks of different origins in the Mokau River in northern Taranaki. The most southern population of black mudfish, a species of entirely northern provenance, occurs in the Mokau, as also does the most northern population of upland bully, a species of entirely southern provenance and in addition, Cran's bully is widespread across the whole area. These sorts of complex patterns, that seem quite frequent across New Zealand, signify distinctive dispersal processes in different groups that share the same habitats.

In the North Island, the northern species of *Paranephrops* is very widely distributed and exhibits a simple pattern that is a contrast with patterns of all species of non-diadromous freshwater fish, all of which are much more localised in range. To graphically illustrate the extent of these contrasts, upland bully, *Gobiomorphus breviceps*, extends north to about the curved line across the North Island (Fig. 19.1), whereas Cran's bully, like the northern *Paranephrops* is very much more widespread across the North Island. So, again, we are seeing contrasting patterns in different taxa across an area that has a single geological and climatic history.

Far southwestern Fiordland (Dusky Sound and Chalky/Preservation Inlet in the southern South Island) has populations of koura, and it is the southern species. This form is widespread across the Southland Plains, where it shares the river systems of the Southland plains with Gollum galaxias, Southland flathead galaxias, and upland bully, none of which is found in the rivers of Fiordland (Fig. 19.1). There is nothing comparable, connecting non-diadromous fish species of Southland to the freshwaters of southern Fiordland: all the fish species present in Fiordland are diadromous. The presence of koura in Fiordland rivers suggests former connections between the rivers there and waterways further east in Southland, perhaps in the Pleistocene when there was a land connection across Foveaux Strait, and shorelines were extended long distances seaward from those now present (Fleming 1979).

Also, whereas many of the non-diadromous fishes of the eastern South Island have penetrated into the intermontane valleys of the eastern Southern Alps (Canterbury galaxias: see Fig. 11.2 – red symbols; alpine galaxias: Fig. 12.2 – green symbols; upland and lowland longjaw galaxias: Fig. 12.3 – black and yellow symbols; upland bully: Fig. 15.2 – blue symbols), the species of koura known from the Canterbury Plains has totally failed to do so (Fig. 19.1); a site in the upper Rakaia River valley results from human translocation (McDowall 2005a).

The apparent disappearance of a perciform fish species once present in New Zealand (known only from a couple of fossil scales – McDowall and Lee 2005 – see Section 1.8, p. 21), and perhaps showing affinities to the Australian fauna, has botanical precedents: there were once casuarinas and eucalypts of Australian types among the New Zealand flora, also in the Miocene of Central Otago (Lee et al. 2001; Gibbs 2006), but they are no longer present here, either.

19.5 Ancient Biotic Elements with Recent Biogeographies

An ancient evolutionary heritage for New Zealand's freshwater fish does not necessarily translate into an ancient distribution pattern, any more than it does for ferns (Brownsey 2001); and how could it, given the dynamic, continually-changing landscape? Wolf et al. (2001) expressed a hope that "it may be possible to identify specific ecological attributes that make a fern group more likely to have retained evidence for vicariance," but many of them seem to be strong dispersers, and so Wolf's hope is unlikely to see fulfilment. Analysis of the biogeography of New Zealand ferns (Brownsey 2001; Perrie and Brownsey 2007) has interesting

similarities to some aspects of freshwater fish distributions – ferns are, of course, ancient like the galaxiid fishes (McDowall 1969; Johnson and Patterson 1996), and they are perhaps much more adept at long distance dispersal (even than diadromous freshwater fish). So it is of interest that Brownsey (2001) argued that some of the most ancient and primitive of all pteridophyte taxa, such as *Lygodium*, *Isoetes*, *Psilotum*, and *Tmesipteris*, have achieved their Australian-New Zealand distributions by dispersal since New Zealand became detached from Gondwana – arguing this on the basis that the fossil record fails to reveal them as present in ancient, late Mesozoic New Zealand, despite them being ancient taxa with long histories elsewhere. Brownsey insisted that the evidence “strongly favours the hypothesis that [many] pteridophytes arrived in New Zealand relatively recently by long distance dispersal”; he estimated that 78% of fern genera first arrived in New Zealand after separation from Gondwana, despite some of them belonging to very ancient lineages. Brownsey (2001) and Perrie and Brownsey (2003) thus recognised the apparent paradox that some member species of an ancient group, like ferns, seem to have a relatively recent presence in New Zealand and, as I have with diadromous fishes, he attributed this to long distance dispersal. And, just as Brownsey (2001) recognised dual or multiple patterns among New Zealand ferns, so too have Pole (1994, 2001), McGlone et al. (2001; McGlone 2006), Lee et al. (2001), and others, for various vascular plants. Wardle (1978) also argued much the same for recent dispersal of various ancient lineages in the New Zealand flora. Lloyd et al. (2003) recognised that in some New Zealand grasses (*Chionochloa* species), strong dispersal ability is a likely prerequisite for large geographical ranges and the same is true of orchids (McGlone 2006; Gibbs 2006). Similar patterns in other plant taxa probably have similar distributions (Sykes and Godley 1968; Pole 1994, 2001). Winkworth et al. (2005) pointed to diverse plant taxa that they considered had reached New Zealand across broad time scales, and from very diverse and distant sources. Even the ‘classic,’ southern Gondwanan tree genus *Nothofagus* (Darlington 1965), described by Lovis (2003) as a “duffer” at dispersal, appears to have attained parts of its broad range in New Guinea, New Caledonia, Australia, Tasmania, New Zealand, and Patagonian South America, by post-Gondwana dispersal (Swenson and Hill 2001; Swenson et al. 2001a, b; Knapp et al. 2005; reviewed in Gibbs 2006). Moreover, Emerson (2008) has explored speciation processes on islands and has concluded that there is a wide diversity of ages of taxa, diversity relating to both the date of arrival of a taxon on an island, and the age of its diversification, summarising that the diversity of taxa on an ancient archipelago may be the product of:

1. Old lineages and ancient speciation
2. Young lineages and recent speciation
3. Old lineages and recent speciation

We do not yet have adequate data on New Zealand’s freshwater fishes to draw similar comparisons, but in principle, all three patterns can be expected, given that New Zealand is an old archipelago.

Emerson’s (2008) distinction illustrates an important biogeographical principle, viz., that taxa with an ancient evolutionary heritage do not necessarily display

distribution patterns that reflect that ancient heritage (McDowall 2008) – and there seems no inherent reason why the distribution patterns of ancient lineages should reflect ancient geologies – though sometimes they may. Morrone and Posadas (2006) with regard to the biogeography of the Falkland Islands ask: “Could anybody be empirically justified in assuming that during the past 130 myr...the most important events in their biotic history were in the last few million years?”, and one might, I suppose, respond “Why not?” (McDowall 2005b). The same general question applies to New Zealand as a whole and, given its turbulent geological and climatic history, there is every reason to think that the impacts of the past few million years have left the greatest imprint on the biota and affecting biotic elements from a wide variety of taxonomic groups.

Brownsey (2001) estimated that about “22% of New Zealand’s pteridophytes are distributed virtually throughout all three main islands” of New Zealand. He concluded that their ranges are not significantly correlated with geographic barriers and considered that the observed patterns result from dispersal around the New Zealand landscape. This alone demands major local dispersal in response to climate change and geological history, a further demonstration that distribution patterns are closely related to species’ ecologies (despite the rejection of this by the panbiogeographers). Just the whole process of invasion of the alpine zone, following glacial retreat, is indicative of how dynamic dispersal processes must have been. Moreover, Brownsey argued that it is unlikely that fern species, shared between New Zealand and other lands, could have remained morphologically undifferentiated in each area since Gondwana and this mirrors arguments I have long raised relating to the likelihood of prolonged morphological stasis for widespread New Zealand galaxiids, such as the inanga (McDowall 1964, 1990, 2002), though Rosen (1974) scorned such notions.

Generalising, an Australian-New Zealand pattern of biotic relationships is common to quite diverse taxonomic groups, with totally different ecologies and evolutionary histories, in which there is this shared Australian-New Zealand nexus, and there is wide agreement that, as with ferns, many of these relationships are an outcome of more recent dispersal events, rather than resulting from ancient (late Cretaceous) vicariant Gondwana connections (though the panbiogeographers, vicariance and cladistic biogeographers apparently do not accept this). Perhaps the most telling aspect of an emerging consensus is the consistent evidence in diverse taxonomic groups for post-Gondwanan connections between the Australian and New Zealand biotas, a connection that must have been an outcome of dispersal (Lee et al. 2001; McGlone 2006; Winkworth et al. 2005; Gibbs 2006; Trewick et al. 2007). Moreover, in addition to its recency, a New Zealand-Australian biotic connection that excludes Patagonian South America is contrary to the customarily-held view that Australia and Patagonia had much later physical contact via their Gondwana connection, than a New Zealand connection to Gondwana (and thus with Australia and Patagonia). However, this is a simplistic argument as there could well have been provincialism in the fauna and flora across the vast expanse of ancient Gondwana, and it is possible that the ancient spatial proximity of Australia and Zealandia in Gondwana may have been more important than the temporal proximity of Australia and South America when part of Gondwana.

Allibone and Wallis (1993) emphasised the opportunity for improved local adaptation once fish populations have forgone diadromy and have lost the potential for the sort of gene flow among populations of conspecifics that hinders local adaptation, and Waters and Wallis (2001) aptly likened the loss of diadromy in freshwater fish to the loss of flight in some insects, and it is also true of birds (see Darlington 1943; Carlquist 1965; Trewick 1997, 2000; Emerson and Wallis 1995; McLellan 1990). Diamond (1990) pointed to comparable loss of flight in several bird lineages that had first arrived in New Zealand by dispersal across the Tasman Sea from Australia – further instances of a deep dichotomy between widespread, highly vagile, colonising species and more localised, derived lineages that have lost their powers of dispersal. These are apt comparisons with New Zealand's non-diadromous freshwater fishes, on a number of grounds – but especially in relation to the loss of the ability to spread, they gained the potential for local genetic differentiation and phenotypic adaptedness, and, in time, speciation. However, there has also been likely vulnerability to local extirpation owing to freshwater habitats being small and ephemeral. Thus recognition that life history (= ecology) is a significant, but divergent, determinant of range in diadromous and non-diadromous New Zealand freshwater fish species, resonates with patterns in some other taxonomic groups.

Several studies of genetic variation and structuring in New Zealand aquatic insects have also explored the role of dispersal, with some unexpected outcomes. Hogg et al. (2002) examined genetic divergence in two flighted aquatic stream insects, both of which they thought would be poor dispersers; one of these insects, however, proved to be almost panmictic from Northland to Otago, suggesting that dispersibility is greater than they had anticipated (and/or genetic divergence very much slower, but perhaps some of both). Smith and Collier (2001) also found unexpectedly low genetic differentiation among populations of another aquatic insect. These insects, having flighted adults (even though some of them have very short-lived adult stages) seem to be more adept at shifting between river catchments than non-diadromous freshwater fish, which are more restricted to freshwater habitats. Thus a role of dispersal in establishing distributions of diverse aquatic biotic elements is increasingly widely touted, as has long been the case for New Zealand's freshwater fishes. Equally, Collier (1993) observed how the impacts of central North Island volcanism on stream insects had been remediated by later reinvasion, resulting in the streams of the Lake Taupo catchment, for instance being rich and diverse, though they exhibit low endemism.

The presence of various non-diadromous fish species (and also koura) on both sides of Cook Strait is strongly at variance with what seems to have happened among some birds – in which there has been divergence of North and South Island endemics, both smaller passerines as well as larger birds like kaka (parrots of the genus *Nestor*) (Heather and Robertson 1996). This might seem surprising, given their powers of flight. Thus, philopatry (Mayr 1963) seems weaker in fluvial fishes than in some volant, forest species, whereas the reverse might have been regarded as more probable; dispersal, it seems, is not always easy, even for birds, though it may relate more to these birds' preferences for continuous forested habitats than to

their ability to fly for only moderate distances. Wardle (1991) identified similar patterns in plants, and reckoned that “Even by a generous estimate, less than 25% of indigenous vascular plants are distributed as widely through the New Zealand mainland as their apparent ecological tolerances would suggest”. The implications of these examples are that historical biogeographical and environmental/ecological processes are both important in understanding distributions patterns, and that patterns are not always simply predictable.

References

- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Apte S, Smith PJ, Wallis GP (2007) Mitochondrial phylogeography of New Zealand freshwater crayfishes, *Paranephrops* spp. *Mol Ecol* 16:1897–1908
- Boyer SL, Giribet G (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *J Biogeog* 36:1084–1099
- Brownsey PJ (2001) New Zealand’s pteridophyte flora – plants of ancient lineage but recent arrival? *Brittonia* 53:284–303
- Buckley TR, Young EC (2008) A revision of the taxonomic status of *Sigara potamius* and *S. limnochares* (Hemiptera: Corixidae), water boatmen of braided rivers in New Zealand. *N Z Entomol* 31:47–57
- Burridge CP, Craw D, Waters JM (2006) River capture, range expansion, and cladogenesis: the genetic signature of freshwater vicariance. *Evolution* 60:1038–1049
- Burrows CJ (1965) Some discontinuous distributions of plants within New Zealand and their ecological significance. Part II. Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. *Tuatara* 13:9–29
- Burrows CJ (1969) Alpine grasslands. In: Knox GA (ed) *The natural history of Canterbury*. Reed, Wellington, N Z, pp 133–166
- Campbell HJ (1998) Fauna and flora of the Chatham Islands: less than 4 my old. *Geol Soc N Z Misc Publ* 97:15–16
- Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland, N Z, 236 pp
- Campbell HJ, Landis CA (2001) New Zealand awash. *N Z Geogr* 51:6–7
- Campbell HJ, Landis CA (2005) Exploring constraints on the antiquity of terrestrial life in New Zealand. *Geol Soc N Z Misc Publ* 119A:12
- Campbell HJ, Trewick S (2003) The Chatham Islands – Noah’s ark or Picton Ferry. *Marsden Fund Update* 25:4
- Campbell H, Begg J, Beu A, Carter A, Curtis N, Davies G, Emberson R, Given D, Goldberg J, Holt K, Hoernli K, Malahoff A, Mildenhall D, Landis C, Paterson A, Trewick S (2009) Geological considerations relating to the Chatham Islands, mainland New Zealand and the history of New Zealand terrestrial life. *Geology and Genes IV. Geol Soc N Z Misc Publ* 126:5–6
- Campos H (1984) Gondwana and neotropical galaxioid fish biogeography. In: Zaret T (ed) *Evolutionary ecology of neotropical freshwater fishes*. Junk, The Hague, The Netherlands, pp 113–125
- Carlquist S (1965) *Island life: a natural history of the islands of the world*. Natural History Press, Garden City, NJ, 451 pp
- Carpenter A (1982) Habitat and distribution of the freshwater shrimp *Paratya curvirostris* (Decapoda: Atyidae). *Mauri Ora* 10:85–98
- Chadderton WL, Ryan PA, Winterbourn MJ (2003) Distribution, ecology and conservation status of Idoteidae (Isopoda) in southern New Zealand. *J R Soc N Z* 33:529–548

- Clarkson BD (1990) A recent review of vegetation development following recent (<450 years) volcanic disturbance in North Island, New Zealand. *N Z J Ecol* 14:59–71
- Clarkson BR, Patel RN, Clarkson BD (1988) Composition and structure of forest overwhelmed at Pureora, central North Island, New Zealand, during the Taupo eruption (c. AD 130). *J R Soc N Z* 18:417–436
- Cockayne L (1917) Notes on New Zealand floristic botany, including descriptions of new species. *Trans Proc N Z Inst* 49:56–65
- Cockayne L (1926) Monograph on the New Zealand beech forests. Part 1. The ecology of the forests and the taxonomy of the beeches. *N Z Forest Serv Bull* 4:1–71
- Collier KG (1993) Review of the status, distribution and conservation of freshwater invertebrates in New Zealand. *N Z J Mar Freshwater Res* 27:339–356
- Cook LG, Crisp MD (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *J Biogeogr* 32:741–754
- Cooper RA (1998) The Oligocene ‘bottleneck’ hypothesis – physical parameters. *Geol Soc N Z Misc Publ* 97:19–22
- Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proc R Soc Lond B Biol Sci* 261:293–302
- Cooper A, Lalueza-Fox C, Anderson S, Rambaut A, Austin J, Ward R (2001) Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* 409:704–707
- Cracraft J (1994) Species diversity, biogeography, and the evolution of biotas. *Am Zool* 34:33–47
- Crandall KA (2000) The monophyletic origin of freshwater crayfish estimated from nuclear and mitochondrial DNA sequences. *Proc R Soc Lond B Biol Sci* 267:1679–1686
- Crandall KA, Fetzner RJ, Lawler SH, Kinnersley M, Austin CM (1999) Phylogenetic relationships among Australian and New Zealand genera of freshwater crayfishes (Decapoda: Parastacidae). *Aust J Zool* 47:199–214
- Craw D, Anderson L, Rieser WJM (2007) Drainage reorientation in Marlborough Sounds, New Zealand, during the Last Interglacial. *N Z J Geol Geophys* 50:13–20
- Craw RC (1979) Generalized tracks and dispersal in biogeography: a response to RM McDowall. *Syst Zool* 28:99–107
- Craw RC (1989) New Zealand biogeography: a panbiogeographic approach. *N Z J Zool* 16:527–547
- Craw R, Heads MJ, Grehan JR (1998) Panbiogeography: tracking the history of life. Oxford University Press, New York, 229 pp
- Croizat L (1952) Phytogeography. Junk, The Hague, The Netherlands, 587 pp
- Croizat L (1958) Panbiogeography – an introductory synthesis of zoogeography, phytogeography and geology: with notes on evolution, systematics, ecology and anthropology, etc. Publ. Author, Caracas, Venezuela, 3 vols
- Croizat L (1964) Space, time, form: the biological synthesis. Publ. Author, Caracas, Venezuela, 881 pp
- Croizat L, Nelson GJ, Rosen DE (1974) Centers of origin and related concepts. *Syst Zool* 23:265–287
- Darlington PJ (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas and the atrophy of wings. *Ecol Monog* 13:37–61
- Darlington PJ (1965) Biogeography of the southern end of the world. Harvard University Press, Cambridge, MA, 236 pp
- Daugherty CH, Gibbs GW, Hitchmough RA (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends Ecol Evol* 8:437–442
- Diamond JM (1990) New Zealand as an archipelago: an international perspective. *Conserv Sci Publ (N Z)* 2:3–8
- du Reitz GE (1960) Remarks on the southern cool temperate zone. *Proc R Soc Lond B Biol Sci* 152:500–507
- Dumbleton LJ (1967) Winter dormancy in New Zealand biota and its palaeoclimatic implications. *N Z J Bot* 5:211–222

- Ebach M, Humphries CJ, Williams DM (2003) Phylogenetic biogeography deconstructed. *J Biogeogr* 30:1285–1296
- Eldon GA (1968) Notes on the presence of the brown mudfish (*Neochanna apoda* Günther) on the West Coast of the South Island of New Zealand. *N Z J Mar Freshwater Res* 2:37–48
- Emberson R (1995) The Chatham Islands beetle fauna and the age of separation of the Chatham Islands from New Zealand. *N Z Entom* 18:1–7
- Emerson BC (2008) Speciation on islands: what are we learning? *Biol J Linn Soc* 95:47–52
- Emerson BC, Wallis GP (1995) Phylogenetic relationships of *Prodontria* (Coleoptera; Scarabaeidae; subfamily Melolonthinae), derived from sequence variation in the mitochondrial cytochrome oxidase II gene. *Mol Phyl Evol* 4:433–447
- Ericson PGP, Chistididis L, Cooper A, Irestedt M, Jackson J, Johansson S, Norman JA (2002) A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc R Soc Lond B Biol Sci* 269:234–241
- Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press, Auckland, N Z, 141 pp
- Gibbs GW (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton, Nelson, N Z, 236 pp
- Grehan JR (1989) New Zealand panbiogeography: past, present and future. *N Z J Zool* 16:513–525
- Haddrath O, Baker AJ (2001) Complete mitochondrial genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proc R Soc Lond B Biol Sci* 268:939–945
- Hansen B, Richardson AMM (2006) A revision of the Tasmanian endemic freshwater crayfish genus *Parastacoides* (Crustacea: Decapoda: Parastacidae). *Invert Syst* 20:713–769
- Harshman J, Braun EL, Braun MJ, Huddleston CJ, Bowie RCK, Chojnowski JL, Hackett SJ, Han K-L, Kimball RT, Marks BD, Miglia KJ, Moore WS, Reddy S, Sheldon FH, Steadman DW, Steppan SJ, Witt CC, Yuri T (2008) Phylogenomic evidence for multiple losses of flight in ratite birds. *Proc Nat Acad Sci* 105:13462–13467
- Heads M (1998) Biogeographical disjunction along the alpine fault, New Zealand. *Biol J Linn Soc* 63:161–176
- Heads M, Patrick B (2003) Biogeography. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) The natural history of southern New Zealand. Otago University Press, Dunedin, N Z, pp 89–100
- Heather BD, Robertson HA (1996) The field guide to the birds of New Zealand. Viking, Auckland, N Z, 432 pp
- Heenan P, Mitchell A (2003) Phylogeny, biogeography and adaptive radiation of *Pachycladon* (Brassicaceae) in the mountains of South Island, New Zealand. *J Biogeogr* 30:1737–1749
- Hill K, Simon C, Marshall D, Chambers G (2009) Surviving glacial ice ages within the biotic gap: phylogeography of the New Zealand cicada *Maoricicada campbelli*. *J Biogeogr* 36:675–692
- Hogg ID, Willman-Huemer P, Stevens MI (2002) Population genetic structure of two New Zealand stream insects: *Archichauliodes diversus* (Megaloptera) and *Coloburiscus humeralis* (Ephemeroptera). *N Z J Mar Freshwater Res* 36:491–502
- Hopkins CL (1970) Systematics of the New Zealand freshwater crayfish *Paranephrops* (Crustacea: Decapoda: Parastacidae). *N Z J Mar Freshwater Res* 4:278–291
- Humphries CJ (2004) From dispersal to geographic congruence: comments on cladistic biogeography in the twentieth century. In: Williams DM, Forey PL (eds) Milestones in systematics. Systematics Association Special Volume Series 67:225–260. CRC Press, Boca Raton, FL
- Hutton FW (1896) Theoretical explanation of the distribution of southern faunas. *Proc Linn Soc N S W* 21:36–47
- Jamieson CD (1998) Calanoid copepod biogeography in New Zealand. *Hydrobiologia* 367:189–197
- Johnson GD, Patterson C (1996) Relationships of lower euteleostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic, New York, pp 251–332

- Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH (2008) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and Palaeobiogeography of the tuatara (*Sphenodon*). *Proc R Soc Lond B Biol Sci* 276:1385–1390
- Knapp M, Stockler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biol* 3:38–43
- Knapp S (2005) Biogeography: space, time, form. *J Biogeogr* 32:3–4
- Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA (2008) The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 143:173–197
- Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust J Bot* 49:341–356
- Lee DE, Bannister JM, Lindqvist JK (2008) Late Oligocene-Early Miocene leaf macrofossils confirm a long history of *Agathis* in New Zealand. *N Z J Bot* 45:565–578
- Leschen RAB, Buckley TS, Harman HM, Shulmeister J (2008) Determining the origin and age of the Westland beech (*Nothofagus*) gap, New Zealand, using fungus beetle genetics. *Mol Ecol* 2008:1256–1276
- Lewis K, Carter L (1994) When and how did Cook Strait form? In: van der Lingen GJ, Swanson KM, Muir RJ (eds) *Evolution of the Tasman Sea basin: Proceedings of the Tasman Sea conference*, Christchurch, New Zealand, 27–30 November, 1992. Balkema, Rotterdam, The Netherlands, pp 119–137
- Lloyd KM, Wilson JB, Lee WG (2003) Correlates of geographic range size in New Zealand *Chionocloa* (Poaceae) species. *N Z J Bot* 30:1751–1761
- Lovis J (2003) When and where did ‘polypodiaceous’ ferns arise? *J Biogeogr* 30:863–964
- Lowe DJ, Green JD (1987) Origins and development of the lakes. In: Viner A (ed) *Inland waters of New Zealand*. Department of Scientific and Industrial Research, Wellington, N Z, pp 1–64
- Lowe DJ, Green JD (1992) Lakes. In: Soons JM, Selby MJ (eds) *Landforms of New Zealand*. Longman Paul, Auckland, N Z, pp 107–143
- Main MR (1989) Distribution and post-glacial dispersal of freshwater fishes in South Westland, New Zealand. *J R Soc N Z* 2:161–169
- Mark AF, Adams NM (1973) *New Zealand alpine plants*. Reed, Wellington, N Z, 262 pp
- Mayden RL (1988) Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Syst Zool* 37:329–355
- Mayr E (1963) *Animal species and evolution*. Belknap, Cambridge, MA, 797 pp
- Mayr E (1982) Processes of speciation in animals. In: Barigozzi C (ed) *Mechanism of speciation*. Liss, New York, pp 1–19
- Mayr E, Diamond JR (2001) *The birds of northern Melanesia: speciation, ecology and biogeography*. Oxford University Press, Oxford, 492 pp
- McDowall RM (1964) The affinities and derivation of the New Zealand freshwater fish fauna. *Tuatara* 12:59–67
- McDowall RM (1969) Relationships of galaxioid fishes, with a further discussion of salmoniform classification. *Copeia* 1969:796–824
- McDowall RM (1970) The galaxiid fishes of New Zealand. *Bull Mus Comp Zool Harv Univ* 139:341–431
- McDowall RM (1971) The galaxiid fishes of South America. *Zool J Linn Soc* 50:33–73
- McDowall RM (1973) Zoogeography and taxonomy. *Tuatara* 20:88–96
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1990) *New Zealand freshwater fishes: a natural history and guide*. Heinemann Reed, Auckland, N Z, 553 pp
- McDowall RM (1996a) Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *J Biogeogr* 23:139–148
- McDowall RM (1996b) Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Can J Fish Aquat Sci* 53(Suppl 1):401–427
- McDowall RM (1998) Driven by diadromy: its role in the historical and ecological biogeography of New Zealand freshwater fishes. *Ital J Zool* 65(Suppl S):73–85

- McDowall RM (2000) The Reed field guide to New Zealand freshwater fishes. Reed, Auckland, N Z, 216 pp
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2004) The Chatham Islands endemic galaxiid: a *Neochanna* mudfish (Teleostei: Galaxiidae). *J R Soc N Z* 34:315–331
- McDowall RM (2005a) Biogeography of the New Zealand freshwater crayfishes (Parastacidae, *Paranephrops* spp.): restoration of a refugial survivor? *N Z J Zool* 32:55–77
- McDowall RM (2005b) Falklands: fact, fiction, fiddlesticks. *J Biogeogr* 32:2187
- McDowall RM (2008) Pattern and process in the biogeography of New Zealand – a global microcosm? *J Biogeogr* 35:197–212
- McDowall RM, Lee DE (2005) Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago New Zealand. *J R S N Z* 35:339–344
- McDowall RM, Stevens MI (2007) Taxonomic status of the Tarndale bully *Gobiomorphus alpinus* (Teleostei: Eleotridae). *J R Soc N Z* 37:15–29
- McDowall RM, Waters JM (2002) A new longjaw galaxias species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. *N Z J Zool* 29:41–52
- McDowall RM, Whitaker AH (1975) In: Kuschel G (ed) The freshwater fishes. Biogeography and ecology in New Zealand. Junk, The Hague, The Netherlands, pp 277–299
- McGlone MS (1985) Plant biogeography and the late Cenozoic history of New Zealand. *N Z J Bot* 23:723–749
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of biota. *Ecol Stud* 186:17–32
- McGlone MS, Duncan RP, Heenan PB (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J Biogeogr* 28:199–216
- McGlone M, Wardle P, Worthy TH (2003) Environmental change since the last glaciation. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C (eds) The natural history of southern New Zealand. Otago University Press, Dunedin, New Zealand, pp 107–128
- McLellan ID (1990) Distribution of stoneflies in New Zealand. In: Campbell IC (ed) Mayflies and stoneflies. Kluwer, Dordrecht, The Netherlands, pp 135–140
- Morrone JJ, Posadas P (2006) Falklands: facts and fiction. *J Biogeogr* 32:2183–2187
- Page RDM (1989) New Zealand and the new biogeography. *N Z J Zool* 16:471–484
- Perrie L, Brownsey PJ (2003) Biogeography of temperate Australasian *Polystichum* ferns as inferred from chloroplast sequences and AFLP. *J Biogeogr* 30:1729–1736
- Perrie L, Brownsey PJ (2007) Molecular evidence for long-distance dispersal in the New Zealand pteridophyte flora. *J Biogeogr* 34:2028–2038
- Pole M (1994) The New Zealand flora – entirely long-distance dispersal? *J Biogeogr* 21:625–635
- Pole MS (2001) Can long-distance dispersal be inferred from the New Zealand plant fossil record? *Aust J Bot* 49:357–366
- Raadik T (2001) When is a mountain galaxias not a mountain galaxias. *Fish Sahul* 15:785–789
- Raadik T (2005) Dorrigo Plateau – a diversity “hot spot” for galaxiids. *Fish Sahul* 19:98–107
- Rosen DE (1974) Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. *Bull Am Mus Nat Hist* 153:265–326
- Rutland J (1888) The fall of the leaf. *Trans Proc N Z Inst* 21:110–120
- Smith PJ, Collier KJ (2001) Allozyme diversity and population genetic structure of the caddisfly *Orthopsyche fimbriata* and the mayfly *Acanthophlebia cruentata* in New Zealand streams. *Freshwater Biol* 46:795–805
- Smith PJ, McVeagh SM, Allibone RM (2003) The Tarndale bully revisited with molecular markers: an ecophenotype of the common bully *Gobiomorphus cotidianus* (Pisces: Gobiidae). *J R Soc N Z* 33:663–673
- Smith PJ, McVeagh SM, Allibone RM (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Soons JM (1992) The West Coast of the South Island. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, N Z, pp 439–455

- Stevens MI, Hogg ID (2004) Population genetic structure of New Zealand's endemic corophiid amphipods: evidence for allopatric speciation. *Biol J Linn Soc* 81:119–133
- Stockler K, Daniel IL, Lockhart PJ (2002) New Zealand kauri (*Agathis australis* (D Don) Lindl, Araucariaceae) survives Oligocene drowning. *Syst Biol* 51:827–832
- Swenson U, Hill RS (2001) Most parsimonious areagrams versus fossils: the case of *Nothofagus* (Nothofagaceae). *Aust J Bot* 49:367–376
- Swenson U, Hill RS, McLoughlin S (2001a) Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. *Taxon* 50:1025–1041
- Swenson U, Backlund A, McLoughlin S, Hill RS (2001b) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* 17:28–47
- Sykes WR, Godley EJ (1968) Transoceanic dispersal in *Sophora* and other genera. *Nature* 218:495–496
- Te Punga MT (1953) The Paryphantidae and a Cook Strait land bridge. *N Z J Sci Tech* 35:51–63
- Thomson GM (1910) Botanical evidence against the recent glaciation of New Zealand. *Trans Proc N Z Inst* 42:348–353
- Trewick SA (1997) Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Phil Trans R Soc (Biol Sci)* 352:429–446
- Trewick SA (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *J Biogeogr* 27:1189–1200
- Trewick SA, Wallis GP (2001) Bridging the beech gap: New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. *Evolution* 55:2170–2180
- Trewick SA, Wallis GP, Morgan-Richards M (2000) Phylogeographical pattern correlates with Pliocene mountain building in the alpine scree weta (Orthoptera, Anostomatidae). *Mol Ecol* 9:657–666
- Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Wallis GP, Trewick SA (2001) Finding fault with vicariance: a critique of Heads (1998). *Syst Biol* 50:602–609
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. *Mol Ecol* 18:3548–3580
- Wardle P (1963) Evolution and distribution of the New Zealand flora as affected by Quaternary climates. *N Z J Bot* 1:3–17
- Wardle P (1978) Origin of the mountain flora, with special reference to trans-Tasman relationships. *N Z J Bot* 16:535–550
- Wardle P (1988) Effects of glacial climates on floristic distribution in New Zealand. 1. A review of the evidence. *N Z J Bot* 26:541–555
- Wardle P (1991) *Vegetation of New Zealand*. Cambridge University Press, Cambridge
- Waters JM, Craw D (2006) Goodbye Gondwana: New Zealand biogeography, geology and the problem of circularity. *Syst Biol* 55:351–356
- Waters JM, McDowall RM (2005) Phylogenetics of the Australasian mudfishes: evolution of an eel-like body plan. *Mol Phyl Evol* 37:417–425
- Waters JM, Wallis GP (2001) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *J Fish Biol* 58:1166–1180
- Waters JM, Craw D, Youngson JH, Wallis GP (2001) Genes meet geology: fish phylogeographic pattern reflects ancient rather than modern drainage patterns. *Evolution* 55:1844–1855
- Willett RW (1950) The New Zealand Pleistocene snow line, climatic conditions, and suggested biological effects. *N Z J Sci Tech* 32B:18–48
- Wilson GDF (2008) Gondwanan groundwater connections of Australian phreatoicidean isopods (Crustacea) to India and New Zealand. *Invert Syst* 22:301–310
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Divers Evol* 8:237–247

- Wolf PG, Schneider H, Ranker TA (2001) Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *J Biogeogr* 28:263–270
- Worthy TH, Hand SJ, Lee MSY, Hutchinson M, Tennyson ADJ, Scofield RP, Marshall BA, Worthy JP, Nguyen MT, Boles WE, Archer M (2009) New Zealand's St Bathans fauna: an update of its composition and relationships. *Geol Soc N Z Misc Publ* 126:40–42
- Young EC (1962) The Corixidae and Notonectidae (Hemiptera: Heteroptera) of New Zealand. *Rec Cauty Mus* 8:327–374
- Zemlak TS, Habit EM, Walde SJ, Battini MA, Adams EDM, Ruzzante DE (2008) Across the southern Andes on fin: glacial refugia, drainage reversals and a secondary contact zone revealed by phylogenetic signal of *Galaxias platei* in Patagonia. *Mol Ecol* 17:5049–5061

Chapter 20

A More Global Perspective and a Final Summation

Abstract New Zealand's earth history and the presence of diadromy have strongly influenced the distributions of its freshwater fishes, in much the same way as they have the fishes of northern temperate lands. There is a deep dichotomy in the biogeographies of diadromous and non-diadromous fishes in the fauna and this, as well as New Zealand's distinctive and enduring geographical isolation, have produced the biota that we observe today. Biogeography can be explored using both top-down and bottom-up approaches. In theory a bottom-up approach provides the ability to explore and synthesise individual patterns in a way that a top-down approach has the tendency to obscure or muffle, and so a bottom-up approach is preferable.

Keywords Bottom-up/top-down • Diadromy • Galaxiidae • Earth history • Synthesis

20.1 New Zealand as Part of Global Ecosystems

Viewing fish distribution patterns across a broader spatial scale than just New Zealand, wide geographical ranges are evident in various other diadromous fish taxa, including northern cool temperate groups such as: lampreys (Petromyzontidae), smelts (Osmeridae), trouts and salmons (Salmonidae), sturgeons (Acipenseridae); eels (Anguillidae) rather more widely across the Indo-West Pacific at tropical to temperate latitudes and widely in the North Atlantic Ocean; and some sicydiine gobies across the tropics and subtropics (Keith et al. 2005; Berrebi et al. 2005). The potential for diadromous fishes to have very broad ranges seems to reflect a general pattern (McDowall 1988). It does not mean that all diadromous species are widely distributed. Many are, but some are not. Brown et al. (1996) recognised a similar phenomenon in marine molluscs; those that do not have a planktonic larval phase in their life cycles (typically having large eggs with much yolk), tend to have smaller ranges than those that with more readily dispersed planktotrophic larvae (which have smaller eggs with little yolk.) This is not a new idea (Thorson 1950; McDowall 1968) and it has wide recognition (Sherman et al. 2008).

Partitioning of a freshwater fish fauna, between diadromous and non-diadromous faunas, in relation to understanding the fauna's historical and ecological biogeography has not, as far as I know, been undertaken to this extent before (but see McDowall 1999 for discussion of the impacts of glaciation on the distributions and genetic diversity of North American freshwater fishes, and McDowall 2008, in which I explore the role of diadromy in generating high species diversity in boreal river systems). New Zealand's freshwater fish fauna is probably unique in its combination of elements in a number of ways, especially:

1. The country's long-lasting and distant geographical isolation
2. The high number and proportion of fish species that are diadromous (and especially the number that are amphidromous)
3. Probably also the level of understanding of the taxonomy, phylogenetic relationships, ecology, and geographical distributions of the species present

The relatively small size of the New Zealand fauna has facilitated the development of that oversight, though it is nevertheless large enough to provide some diversity in ecology, life history, distribution and phylogenetic relationships. Thus, it is quite possible that what I have been able to demonstrate here for New Zealand may rarely be achievable for freshwater fish faunas elsewhere. To the extent that the explicitness of the dichotomy between diadromous and non-diadromous species is rarely available, so also will be the clarity of the conclusions achievable. Be that as it may, I have little doubt that the principles explored here have broad applicability. Parts of the distributions of biotas will be driven largely by ecology and dispersal and other parts will have distributions that derive primarily from vicariance processes and earth history, though the latter are often affected by local re-dispersal processes after relevant vicariance events have taken place as climate and geology continue to change. Some country's/region's biotas appear to have entirely dispersal origins, as on many of the isolated islands of the globe, islands that are often quite young (Wagner and Funk 1995; Thornton 2001; Wolf and Schneider 2001; Gillespie 2002; Kingston et al. 2003; McDowall 2003, 2004, 2005). On the other hand, I would be very surprised if the distribution pattern/biogeography of any biota is driven entirely by vicariance, since dispersal is such a universal phenomenon, at least at a local scale.

The freshwater fish fauna of Hawaii is well known, though there are just five species, all of them diadromous (amphidromous) (Radtke and Kinzie 1991; Zink 1991; Zink et al. 1996; Chubb et al. 1998; Fitzsimons et al. 2002), and analysis demonstrates the broad impacts of life at sea on distributions and diversity in that fauna, as in New Zealand (McDowall 2003, 2007). Similar patterns are likely in Guam, where a high proportion of the fauna is diadromous (Fitzsimons et al. 2002), and the same may be true more widely where there are numerous diadromous gobies, especially for islands in the central western Pacific, the western Indian Ocean, and the Caribbean (Maciolek and Ford 1987; McDowall 1988; Bell et al. 1995; Fievet 2000; Buden et al. 2001; Berrebi et al. 2005; Hoareau et al. 2006). Similar patterns of differential penetration, with some species moving further up stream than others, are also likely to be present. What is known of the distributions

of freshwater fishes in Hawaiian streams clearly identifies major differences in the extent to which the species penetrate inland, the extreme case being *Lentipes concolor*, which is known, when migrating upstream from the sea, to climb falls to a total of >600 m, whereas *Eleotris sandwichensis* demonstrates no ability to climb falls or even swift rapids or torrents, and is found almost exclusively at very low elevations (Englund and Filbert 1997; Fitzsimons et al. 2002). For these faunas, similar patterns of diversity and distribution to those discussed here for the New Zealand fauna, are likely to emerge, as the island faunas and their distributions become better known. Possibly the Japanese fauna may be amenable to this sort of analysis, given the substantial number of diadromous fishes there, with lots of salmonids, osmerids, cottids and gobioids (Okada 1960).

Heaney et al. (2005) have reviewed the biogeography of mammals across the Philippine archipelago and, though the mechanisms they describe as affecting distribution are different from those discussed here for the New Zealand freshwater fish fauna, the principles are much the same. They suggested, for instance, that a “multi-species comparative approach should be the most useful for detecting the role of ecological and historical factors in generating pattern...helping to distinguish their relative importance and determining the manner in which they interact to produce phylogenies and patterns of biological diversity”. Moreover, they thought that the “integration of the two perspectives” was essential. Their analysis was related to two attributes:

- One geological (historical), viz., the extent to which islands may have been joined to each other, or not, in the relatively recent past
- The other ecological, viz., the ability of species to move across ocean gaps between islands

They thought that “...any attempt to make general statements about rates of genetic change between populations must take into account the ecological attributes of the species in question” – a perspective diametrically different from those of panbiogeographers like Croizat (1964), Page (1989), Craw (1989) and Grehan (1989), who have argued vehemently that distribution patterns do not reflect the ecological attributes of species, and seem to buttress their arguments on the basis of some carefully (strategically) selected species in which this may be true (see below).

There is clearly a sense in which my data on New Zealand’s diadromous and non-diadromous fish species draw the same contrast, except that in Heaney et al.’s (2005) account dispersal processes tend to be primarily ‘one-off’ historical events, whereas with New Zealand’s diadromous species, the dispersal processes are continual, annually-replicated, cohort-scale events – year after year after year, one cohort after another....

Heaney et al. (2005) considered it “an intuitively obvious explanation that a non-volant mammal should have rates of dispersal across water barriers orders of magnitude lower than those of volant mammals”, and the same intuition applies to comparisons of diadromous and non-diadromous freshwater fish – in which the dichotomy is very deep. Moreover, just as Heaney et al. (2005) identified substantial genetic differentiation among the weak colonisers, so also have molecular studies of a wide diversity

of New Zealand's freshwater fish identified genetic structuring in populations across the geographical ranges of non-diadromous species: by Allibone and Wallis (1993) for non-diadromous galaxiids generally; by Ling and Gleeson (2001) and Davey et al. (2003) for *Neochanna* mudfishes; by Waters and Wallis (2001) for the *Galaxias vulgaris* species complex; by Smith et al. (2005) and Stevens and Hicks (2009) for *Gobiomorphus* bullies; by Waters and Craw (2008) for the longjaw galaxias species; by Waters et al. (2006) for dwarf galaxias; and also by Apte et al. (2007) for New Zealand's freshwater crayfish, genus *Paranephrops*. Similar patterns can be seen for freshwater fishes in other lands (see Zink et al. 1996; Chubb et al. 1998 in Hawaii; Berrebi et al. 2005 in Reunion). Heaney et al. (2005) argued that the "question of geological history or ecology is based on a false premise that only one or the other is a significant factor; in this case both are highly important and we predict that both will be found to be equally important in all other island archipelagos" – another instance of May's (1986) false dichotomies in ecology. And so it is for New Zealand's freshwater fish fauna.

Essentially, it seems to me that there is a global biogeographical continuum.

- At one end of that continuum are highly isolated, geologically young oceanic islands that have never had any other land connections, in which the entire biotas have been assembled by dispersal processes, as in Hawaii and many other, often tropical or subtropical islands or island archipelagos (Wagner et al. 1995; Price and Wagner 2005; McDowall 2003, 2004), but including others like the sub-Antarctic Falkland Islands as well (McDowall 2005).
- At the other extreme in this continuum are some continental land masses where, in theory, it is possible that the entire biota has been assembled by vicariance processes – though a total absence of dispersal seems, to me, extraordinarily unlikely.

Between these extremes there is bound to be a continuum in which the roles of dispersal and vicariance are reciprocal – the role of one rises as the role of the other falls. The key element is to be able to discriminate between the various processes and in general this will not be easy, though it is relatively easy when comparing New Zealand's diadromous and non-diadromous fishes, as with Heaney et al.'s (2005) volant and non volant mammals.

There is an important issue of principle, here.

20.2 A Biogeographical Dichotomy

What emerges most explicitly from this study is that the distributions of New Zealand freshwater fishes reflect two very different biogeographies. The different patterns drawn here are deep and fundamental, both ecologically and biogeographically – the fauna can be partitioned into two ecologically distinct groups, the contents of which each bear no explicit connection to phylogenetic groupings in the fauna. Instead, they cut across phylogenetic relationships. Each group is characterised primarily and substantially, by differences in life history strategies, involving whether fish are diadromous, or not.

- Diadromous species have a dispersal biogeography: diadromy giving species a powerful ability both to spread and to promote recovery from perturbation (of which New Zealand has had plenty) – life appears to evolve independently of earth history: vast numbers of fish at sea, cohort by cohort, year after year, provide very powerful ability to spread around New Zealand at the local spatial scale, and around the Southern Hemisphere at a more global scale.
- Non-diadromous species have distribution patterns that often conform to independently authenticated historical geological and climatic changes across New Zealand history, although there is a wide lack of congruence among patterns in various taxonomic groups, as if their distributions have been mediated by different geological and climatic processes, even among non-diadromous species, but undoubtedly also reflect individualistic dispersal processes across the New Zealand landscape, i.e., even when the driver seems to have been vicariance, distribution patterns differ from one taxonomic group to another.

Thus, within one biota we can see both dispersal and vicariance processes at work simultaneously, in two fractions of the fauna, one driven by ecology (migration) and the other by history. Brown et al. (1996) believed that “the apparent division between ‘ecological’ and ‘historical’ biogeography inhibits a thorough synthetic understanding of the patterns of distribution, and the contemporary and historical processes that have produced them”, and they sought the “emergence of a synthetic perspective”. Besides, Lieberman (2003) opined that “It has been repeatedly demonstrated that dispersal as traditionally defined, has little validity as a general explanation of historical biogeographical patterns”. My results for New Zealand’s freshwater fishes negate both assertions.

Lester et al. (2007) explored data on marine organisms for a relationship between dispersal ability and geographic range size, and though they found evidence for such a relationship, they cautioned that “attention should be paid to other processes responsible for variation in range size. What is clear from data on the distributions of New Zealand freshwater fishes is that the dichotomy in pattern caused by the presence or absence of diadromy, does generate a dichotomy in range sizes, with non-diadromous species having much narrower ranges: diadromous species have larger ranges driven by dispersal through coastal seas, there has been little speciation, and any that there has been is masked by their high dispersal ability. In contrast, non-diadromous species have distinctly narrower ranges, there is evidently little dispersal going on, with the result that there has been rather more speciation which can in many instances be related to landscape history and geology. Moreover, variation in range size in the diadromous species, once they have left the sea and occupied freshwater habitats appears to be substantially driven by migratory ability and instinctive migratory drives, with certain species being more aggressive migrators and having substantially broader distributions that extend long distances inland within river systems, whereas others have rather narrower distributions and may extend inland for only small distances.

Page (1989), Craw (1989) and Grehan (1989) all seemingly approved of Croizat’s (1964) questioning of “the conventional wisdom that the distribution

patterns of organisms with greatly differing ecologies are very different” (Page 1989). My results, when comparing the distributions of diadromous and non-diadromous New Zealand freshwater fishes, demonstrate that this conventional wisdom is certainly correct, at least in some instances. I suspect that it is probably generally correct. The present study shows that it is impossible to thoroughly understand the biogeography of the New Zealand freshwater fish fauna without careful partitioning the fauna across two divergent life history strategies, i.e. based on their ecology.

McGlone (2006) has explored this question in considerable detail for New Zealand plants – finding that:

- Asexual and clonal species are good at dispersing, needing only small propagules.
- That wetland plants seem to spread, perhaps associated with highly dispersive wetland birds.
- That plants with very fine, almost dust like spores and seeds, like ferns, mosses and orchids are highly dispersive.
- That plants with hooked, barbed or sticky seeds are disproportionately involved in dispersal.
- And that there is a distinct contrast of poor dispersal by forest trees, such that all New Zealand conifers are endemic.

In addition, the species that are tending to find their way to New Zealand are very often birds, in at least some instances their arrival and success perhaps being associated with ecosystem changes that make New Zealand habitats more welcoming for certain types of birds. And so, despite the negative assertions of the panbiogeographers, there clearly is a connection between ecology and distribution, both for a wide diversity of plant and animal taxa, including New Zealand’s diadromous freshwater fishes.

Moreover, there are many instances where biotas are heavily represented by species that are highly vagile, this being an important aspect of biotic dispersal (Kodandaramaiah 2009). Heaney et al. (2005) concluded that “geological history and ecological traits produce interactive processes, and must be considered simultaneously for accurate conclusions about general genetic processes in nature to be produced.” Essentially, they drew deep distinctions between strong fliers with high colonising ability and weak fliers with low colonising ability. Shepherd et al. (2009) drew attention to the number of plant groups with windborne seeds or other dispersive seeds on the Chatham Islands, about 800 km east of mainland New Zealand, and recall that geologists think these islands were submerged by sea only a few million years ago (Campbell and Hutchings 2007). The same is probably true of the Auckland and Campbell Islands, well to the south of New Zealand. Boyer and Giribet (2009: 1085) reckoned that “The evolutionary history of most plant and animal groups has been studied with a focus on a single biogeographic process such as vicariance, dispersal or radiation,” but I think that, too, is incorrect. It seems to me that most biogeographers, apart from those with a particular, almost doctrinaire commitment to some particular ‘method’ have genuinely sought to identify

the most likely causes behind our understanding of distribution patterns. As the present study emphasises, there have been divergent roles for both dispersal (relating to the external origins of the freshwater fish fauna and to the generation of pattern among diadromous species) and vicariance (insofar as patterns of non-diadromous species across the New Zealand landscape are concerned).

Of some particular interest is the likelihood that there is a process going on in the New Zealand freshwater fish fauna in which there is a shift between diadromous and non-diadromous life cycles at both individual species (landlocking) and species group levels, and as this shift takes place, the basis for the fauna's biogeography tends to shift from ecological to vicariance processes.

One of the perhaps surprising points that emerges from a study of pattern across the fauna, among complexes of non-diadromous species, comparing different species complexes, is that there seems to be little congruence – each species complex seems to have its own pattern of dispersal, diversification and speciation, and although the species complexes occupy the same general landscapes, their responses to landscape changes are highly individualistic. Unmack (2009: A389) found much the same for the Australian freshwater fish fauna, observing that “Over-arching biogeographic hypotheses are inadequate to explain the independent histories of each group ... that ... independent biogeographic patterns are common...[and that] finding broader explanations for patterns may be the exception rather than the rule.” Moreover, he found that “When phylogeographic patterns for each fish group were combined, there was little congruence in their patterns of divergence across Australia despite a high degree of co-occurrence.”

Wallis and Trewick (2009: 3,555–6) found “a consensus emerging that dispersal has been a major process leading to the formation of the [New Zealand] flora and fauna....Indeed some have gone further and questioned whether there are necessarily any truly Gondwanan elements in New Zealand”, citing Pole (1994, 2001) Waters and Craw (2006), Trewick et al. (2007), Goldberg et al. (2008) and Landis et al. (2008). I am unsure that these cited authors have gone quite this far, and elsewhere cite a considerable diversity of taxa, mostly animals and many of them either aquatic or dependent on moist environments such as forest litter, and in which dispersal might seem unlikely.

20.3 Is New Zealand a Special Case?

It might be asserted that the New Zealand situation is a special case, and perhaps it is in some details:

- To the extent that New Zealand is both an island and a continent (Darwin 1859; Wallace 1880; Diamond 1990; Gibbs 2006).
- To the extent that partitioning of its fauna is so clear and unequivocal.

I suspect, however, that there are similar dichotomies in all biotas – although their partitioning may be less explicit than between the diadromous and non-diadromous

freshwater fishes of New Zealand. To the extent that this is true, some separation of ecological and historical aspects of biotas may be essential for achieving the synthetic understanding of their biogeographies that Brown et al. (1996) (and most other biogeographers) are seeking.

Price and Wagner (2005) drew a distinct contrast in the Hawaiian flora, in which they thought that some plants elements disperse widely and rapidly owing to birds eating their fruit, and in which a “large number of species-poor lineages include disproportionate numbers of wide-ranging ... species”. In some ways the patterns they described resemble what is reported here for diadromous freshwater fish. In both these Hawaiian birds and New Zealand freshwater fishes, high dispersal rates derive from ecology and result in broad distributions, and suppress divergence and speciation. Interestingly, the very modest Hawaiian freshwater fish fauna (five gobioids, all of them amphidromous) exhibit patterns that resemble those in the diadromous New Zealand freshwater fish fauna – species are widespread across the archipelago, are widely sympatric at least at the catchment scales, and there has been no local diversification, nor is there evidence for genetic structuring across species’ ranges (Zink 1991; Zink et al. 1996; McDowall 2003).

Wilkinson (2003) drew attention to Ebach and Humphries’ (2003) assertion that “the dynamic view of the Earth produced by our understanding of plate tectonics is central to biogeography, and [that] dispersal-centred explanations are largely an outdated survivor from a static view of the earth”, and he expressed his disagreement with that conclusion; I agree absolutely with Wilkinson, based on my partitioning of the New Zealand freshwater fish fauna into diadromous/non-diadromous dispersal and vicariant components. My view is supported by the molecular studies of Waters and Wallis (2001), who considered that their studies are revealing the shortcomings of solely distribution-based panbiogeographic analyses, and dispersal is a key element in the biogeography of the freshwater fish fauna. Increasingly, the same is being shown for the New Zealand flora (Winkworth et al. 1999, 2005; Gibbs 2006; McGlone 2006).

Wilkinson (2003) thought, also, that even at “scales that appear ideal for vicariance-inspired explanations, dispersal can turn out to provide a better answer”; and once again, my analyses of the New Zealand freshwater fish fauna support that view, as well as for taxonomic groups more widely (McDowall 2002, 2003; Price and Wagner 2005) – dispersal seems to explain the distributions of the more widespread species, whereas vicariance processes may have controlled the distributions of species and species groups across narrower geographical ranges. Furthermore, Wilkinson (2003) remarked that: “Darwin (1859) may have showed great good sense in emphasizing the importance of dispersal, not merely because he did not know about plate tectonics, but because dispersal is a fundamental process in understanding much of biogeography”. Once again, this is consistent with what I have described here. Dispersal is a key element in generating pattern and it, of course, facilitates the achievement of wide ranges, as well as inhibiting evolutionary divergence through fostering gene flow – one of the ‘drivers’ of wide-ranging distributions is the fact that the gene flow facilitated by dispersal counteracts genetic divergence relating to local adaptation.

Ricklefs and Schluter (1993), recognised that “Geographical, evolutionary and historical factors play a strong role in determining a community’s composition, diversity, niche responses and perhaps other attributes of its organization...[and they thought that] ecologists must now reject the parochial view of local determinism and recognize that ecology, evolution, geography and history are different facets of a single set of processes and the patterns they generate”. Thus over a wide front in ecology and biogeography, there is a strong plea for multi-faceted approaches that may lead to a more holistic view of the way biotic distributions are generated and understood. Riddle (2005) asserted that in some situations “...the dichotomy between an ecological vs. historical biogeography simply does not track the many patterns and processes considered relevant and worthy of our attention.... The current revolution should bring an end to the protracted identity crisis [in biogeography] by replacing the ecological and historical biogeographies of the twentieth century with an integrated biogeography for the twenty-first century”. It would be real progress if this were so. To achieve this there is a need to set aside doctrinaire, all-or-nothing attitudes and to address the diversity of both process and pattern: we are dealing with one biota, one geological, landscape/climatological history and one, small, distributional scenario, but many processes.

Brown et al. (1996) expressed a hope that “ultimately it will be possible to explain most of the variation in any particular species with a model of how spatial and temporal variation’s limiting niche parameters affect local and regional population dynamics”. They were clearly looking to ecology to explain local patterns of distribution. Humphries (2000), adopted a totally different perspective, asserting that “When the historical components are adequately investigated, most, if not all, the large-scale distributions will be explained”, and that “this would have a more fruitful outcome than the supply of individual stories for every different group of taxa”. I believe that the present account shows that the generalities of neither Brown et al. (1996) nor Humphries (2000) are universally true. But, above all else, it points to an end to the general applicability of Humphries’ hope: I suspect that there are few or no universal explanation. In some instances individual distribution/speciation patterns reflect earth history, as is, to some extent, true in New Zealand’s non-diadromous fishes, though even in these, there are marked contrasts in patterns and processes between species groups across the same landscape history. There are typically no universal stories, and this is a likely outcome of the chance nature of much dispersal, even across species groups, though there are some similarities in detail. As for diadromous species, the individual stories do combine to tell a consistent corporate story – the repeated patterns are due to a common element in their ecologies, and are an outcome of their dispersal, i.e. migrations to and from the sea provide species with the concomitant ability to spread across a landscape in a way that would not be possible were they restricted to fresh water. This is a consistent explanation of what is a consistent pattern, it is driven by diadromy, and has nothing to do with earth history (McDowall 1998). Patterns are a product of proximate ecological, cohort-scale processes, ever repeating.

Humphries (2000, 2004) has expressed disinterest in individual ‘stories’ and reckoned that biogeography is not about dispersal. He thought that an: “ecologist’s view

is shaped by consideration of the factors that shape distributions on short time scales, the effects of climate and processes such as migration and immigration in particular localities”, whereas: Historical biogeographers concentrate more on the deeper history and are concerned more with the large-scale patterns over geological time”.

However, the problem is that with the passage of time, ecological events become history, and there are no non-historical ecological or dispersal events. As we are building up our knowledge of history, of the record of what survives from what has happened in the past, we are finding that much of what has happened was driven by ecology. It seems to me, from observing what is happening in our contemporary world, that it is unlikely that any biota will have an entirely vicariance explanation as there is always scope for dispersal. There will, however, continue to be a general problem of partitioning the faunas between one and the other. Humphries (2004), discarded dispersal as being “Anomalies due to a variety of historical reasons [which] can be catered for without assuming any dispersal, vicariant events or extinction events”, and he reckoned that “cladistic biogeography is the only [method] that has attempted to develop a purely pattern approach to overcoming the problems of dispersal, vicariance and extinction by systematic means”. As is so often said, what one sees depends on where one is looking from. Clearly Humphries’ view is very different from mine, and from my viewpoint, Humphries is quite simply wrong.

Humphries and Parenti (1999) insisted that we should be seeking area relationships as the foundations for biogeography and that various land connections ought to be the primary focus in establishing biotic distributions. This may be so for some components of some biotas, as with New Zealand’s non-diadromous freshwater fish species. It is, however, totally inappropriate and inapplicable for others as, for instance, where the diadromous species are concerned, and where such an approach is at best fruitless and probably misleading. The clarity of the partitioning of the New Zealand freshwater fish fauna in such an explicit, unequivocal way, as discussed here, is perhaps unusual, but I suspect similarly diverse explanations of many other biotas would apply if they could similarly be partitioned.

20.4 Biogeography: Top Down or Bottom Up – Again?

The fundamental differences, in the end, relate to whether patterns are explained by top-down or bottom-up processes. Clearly Brown et al. (1996) favoured a bottom up approach (looking for accumulating general patterns across individual cases), whereas Humphries and Parenti (1999) and Humphries (2004) seemed adamant that a top-down approach is needed (they seek to discover pattern from the big picture, having expressed a lack of interest in individual patterns). My analysis shows that at least for diadromous taxa a bottom-up approach is both appropriate and essential. I would argue, further, that a bottom-up approach ought always be fruitful in all biogeography, insofar as species’ distributions are individualistic entities formed by each species’, or species group’s highly individualistic response to earth and ecological history. A biota has no singular history as an entity: rather, the

whole is the sum of its parts, some of it a result of vicariance, some of it generated by dispersal (McDowall 1978). Moreover, it ought to always be possible to derive general patterns of area relationships (Humphries' passion) by the use of a bottom up approach, insofar as the overall patterns are basically established, in nature, by the summation of individual patterns. The patterns reflected by individual species in monophyletic species-groups reflect the history of individual entities that basically bear no historical/genealogical relationships to other entities – the similarities in the general patterns are the outcome of individualistic responses to earth history, and these are what interest me. If patterns are a product of earth history, this will reveal itself by the congruence of patterns in multiple monophyletic taxonomic groups across the biota. Following Humphries (2000, 2004), and imposing a top-down approach that tends to force individual patterns to conform to perhaps majority agreement can only result in a significant loss of biogeographical clarity, even if it provides some comforting uniformity. A 'popularity contest' seems, to me, a strange way to define history.

Thus, the Croizatian (Croizat 1952, 1958, 1964) mantra that "earth and life evolve together", is at best a half truth. Holloway (2003) summarised that "The potential survivors in an ever changing and evolving archipelago will show life zone fidelity or terrane fidelity according to their innate capacities for dispersal or their ecological and genetic flexibility....Our approach certainly for terrestrial organisms must acknowledge that patterns may develop both through the movement of organisms and of the substrate on which they exist, and therefore our methodology must be such as to foreclose on neither option, but must discriminate between them". This is precisely the scenario presented by New Zealand's freshwater fishes. For Humphries (2004) it seems clear that "Biology and distributions of organisms are inextricably linked", but that assumption is beset with proscribing what parts of their "biology" are so linked. In the end, the consensus is that at least New Zealand's galaxiid fishes have a derivation intimately associated with transoceanic dispersal, despite the apparent Gondwanan pattern that the galaxiid and related fishes display around the cool-temperate Southern Hemisphere (Burridge et al. 2009).

Clearly, as far as the galaxiids as a whole are concerned 'earth and life' did not evolve together although, equally, it is apparent that this mantra is in part true when we examine more localised patterns in the non-diadromous components of the fauna. This makes for another interesting irony, in that the more widely distributed taxa, which we might expect to reflect earth history, in fact don't, whereas taxa that are more locally distributed, and in which dispersal might seem more easily accomplished do, to some extent, conform that that statement.

20.5 Answering Darwin's Question

Darwin (1859) long ago asked: "Who can explain why one species ranges widely and is very numerous and why another allied species has a narrow range and is rare?" At least for New Zealand freshwater fishes, part of the explanation for these

differences lies in their divergent life history strategies, and is thus related to differences in their behavioural ecology. If Humphries (2004) were to search for patterns of congruence in the New Zealand freshwater fish fauna he would find congruent patterns among the diadromous species that are virtually identical – they are essentially New Zealand wide (even though their inland penetration differs) and the pattern is driven by dispersal.

There are other patterns in the non-diadromous components in the fauna, in which there is little, or no, congruence from one species group to another: different species complexes display quite different patterns, and though patterns in each complex seem to be driven by earth history; the surprising thing is that there are different patterns in each species complex, though they seem to be the outcome of the same earth history – that seems paradoxical – the patterns are individualistic for different taxonomic groups or lineages. Interestingly, Thacker et al. (2008) in exploring the phylogeography of two small, eastern Australian eleotrids of the genus *Philypnodon*, found that although there seemed strong connectivity between internal and coastal river drainages involving several taxa in the same region, “there appears little evidence for phylogeographic patterns that are congruent in time and space, as genetic divergences across these drainages are often quite different. There is equally a lack of congruence across taxa in New Zealand, and more so, catchment connections seem often to have facilitated the spread of some species but not others. Patterns of spread are clearly complex, and we have quite possibly only just begun to explore the relationship between river catchment connections and taxonomic diversity. Cracraft (1994) thought that “we can expect biotic dispersal, itself, to leave a sympatry of historical imprints on the evolution of species assemblages... even a biotic assemblage of small spatio-temporal scale is composed of species whose presence reflects the spatial history of endemism within which the assemblage is embedded.” It is simply not always so.

References

- Allibone RM, Wallis GP (1993) Genetic variation and diadromy in some New Zealand galaxiids (Teleostei: Galaxiidae). *Biol J Linn Soc* 50:19–33
- Apte S, Smith PJ, Wallis GP (2007) Mitochondrial phylogeography of New Zealand freshwater crayfishes, *Paranephrops* spp. *Mol Ecol* 16:1897–1908
- Bell KNI, Pepin P, Brown JA (1995) Seasonal, inverse cycling of length- and age-at recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies. *Can J Fish Aquat Sci* 52:1535–1545
- Berrebi P, Cattano-Berrebi G, Valade P, Ricou J-F, Hoareau T (2005) Genetic homogeneity in eight freshwater populations of *Sicyopterus lagocephalus*, an amphidromous gobiid of La Réunion Island. *Mar Biol* 148:179–188
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries and internal structure. *Ann Rev Ecol Syst* 27:597–623
- Boyer SL, Giribet G (2009) Welcome back New Zealand. regional biogeography and Gondwanan origin of three independent genera of mite harvestmen (Arachnida, Opiliones, Cyphophalmi). *J Biogeogr* 36:1084–1099

- Buden DW, Lynch DB, Watson RE (2001) The gobiid fishes (Teleostei: Gobioidae: Sicydiinae) of the headwater streams of Pohnpei, Eastern Caroline Islands, Federated States of Micronesia. *Micronesica* 34:1–10
- Burridge CP, McDowall RM, Craw D, Wilson M, Waters J (2009) Does Gondwanan vicariance explain any aspect of contemporary galaxiid (Euteleostei: Galaxiidae) distribution? 8th Indo-Pac Fish Conf & 2009ASFB Worksh & Conf 31, May–5 June, 2009, Fremantle WA. p. A34
- Campbell HJ, Hutchings G (2007) In search of ancient New Zealand. Penguin, Auckland, 239 pp
- Chubb AL, Zink RM, Fitzsimons JM (1998) Patterns of mtDNA variation in Hawaiian freshwater fishes: phylogeographic consequences of amphidromy. *J Hered* 89:8–16
- Cracraft J (1994) Species diversity, biogeography, and the evolution of biotas. *Am Zool* 34:33–47
- Craw RC (1989) New Zealand biogeography: a panbiogeographic approach. *N Z J Zool* 16:527–547
- Croizat L (1952) *Phytogeography*. Junk, The Hague, The Netherlands, 587 pp
- Croizat L (1958) *Panbiogeography – an introductory synthesis of zoogeography, phytogeography and geology: with notes on evolution, systematics, ecology and anthropology, etc.* Publ. Author, Caracas, Venezuela, 3 vol
- Croizat L (1964) *Space, time, form: the biological synthesis*. Publ. Author, Caracas, Venezuela, 881 pp
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray, London, 502 pp
- Davey ML, O'Brien L, Ling N, Gleeson DM (2003) Population genetic structure of the Canterbury mudfish (*Neochanna burrowsius*): biogeography and conservation implications. *N Z J Mar Freshwater Res* 37:14–22
- Diamond JR (1990) New Zealand as an archipelago: an international perspective. *Conserv Sci Publ (N Z)* 2:3–8
- Ebach M, Humphries CJ (2003) Ontology of biogeography. *J Biogeography* 30:959–962
- Englund R, Filbert R (1997) Discovery of the native stream goby, *Lentipes concolor*, above Hawaii's highest waterfall, Hi'ilawe Falls. *Bish Mus Occ Pap* 49:62–64
- Fievet E (2000) Passage facilities for diadromous freshwater shrimps (Decapoda: Caridea) in the Banaier River, Guadeloupe, West Indies. *Regul Riv – Res Man* 16:101–112
- Fitzsimons JM, Parham JE, Nishimoto RT (2002) Similarities in behavioral ecology of amphidromous and catadromous fishes on the oceanic islands of Hawai'i and Guam. *Environ Biol Fish* 65:123–129
- Gibbs GW (2006) *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton, Nelson, N Z, 236 pp
- Gillespie RB (2002) Biogeography of spiders on remote oceanic islands of the Pacific: archipelagos as stepping stones. *J Biogeogr* 29:655–662
- Goldberg J, Trewick SA, Paterson AM (2008) Evolution of the New Zealand terrestrial fauna: a review of molecular evidence. *Phil Trans R Soc Lond B Biol Sci* 363:3319–3334
- Grehn JR (1989) New Zealand panbiogeography: past, present and future. *N Z J Zool* 16:513–525
- Heaney LR, Walsh JS, Peterson AT (2005) The roles of geological history and colonization abilities in genetic differentiation between mammalian populations in the Philippine archipelago. *J Biogeogr* 32:229–247
- Hoareau T, Bosc P, Valade P, Berrebi P (2006) Gene flow and genetic structure in *Sicyopterus lagocephalus* in the south-western Indian Ocean, assess by intron-length polymorphism. *Exp Mar Biol* 349:223–234
- Holloway JD (2003) An addition to southeast Asian biogeography. *J Biogeogr* 30:161–163
- Humphries CJ (2000) Form, space and time: which comes first? *J Biogeogr* 27:11–16
- Humphries CJ (2004) From dispersal to geographic congruence: comments on cladistic biogeography in the twentieth century. In: Williams DM, Forey PL (eds) *Milestones in systematics*. Syst Assoc Spec Vol Ser 67:225–260. CRC Press, Boca Raton, FL
- Humphries CJ, Parenti LR (1999) *Cladistic biogeography: interpreting patterns of animal and plant distributions*, 2nd edn. Oxford University Press, Oxford, 187 pp

- Kodandaramaiah U (2009) Vagility: the neglected component in historical biogeography. *Evol Biol* 36:327–335
- Keith P, Galewski T, Cattaneo-Berrebi G, Hoareau T, Berrebi P (2005) Ubiquity of *Sicyopterus lagocephalus* (Teleostei: Gobioidae) and phylogeography of the genus *Sicyopterus* in the Indo-Pacific area inferred from mitochondrial cytochrome b gene. *Mol Phyl Evol* 37:721–732
- Kingston N, Waldron S, Bradley U (2003) The phylogeographical affinities of the Pitcairn Islands – a model for south-eastern Polynesia? *J Biogeogr* 30:1311–1328
- Lester SE, Rutenburg BI, Gaines SD, Kinlan BP (2007) The relationship between dispersal ability and geographic range size. *Ecol Lett* 10:745–758
- Landis CM, Campbell HJ, Begg RJ, Mildenhall DC, Paterson AM, Trewick SJ (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol Mag* 145:173–197
- Lieberman DS (2003) Paleobiogeography: the relevance of fossils to biogeography. *Ann Rev Ecol Syst* 34:51–69
- Ling N, Gleeson DM (2001) A new species of mudfish, *Neochanna* (Teleostei: Galaxiidae) from northern New Zealand. *J R Soc N Z* 31:385–392
- Maciolek JA, Ford JJ (1987) Macrofauna and environment of the Nanpil-Kiepw River, Panape, Eastern Caroline Islands. *Bull Mar Sci* 41:623–632
- May RM (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology* 67:1115–1126
- McDowall RM (1968) Oceanic islands and endemism. *Syst Zool* 17:346–350
- McDowall RM (1978) Generalized tracks and dispersal in biogeography. *Syst Zool* 27:88–104
- McDowall RM (1988) Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London, 309 pp
- McDowall RM (1998) Driven by diadromy: its role in the historical and ecological biogeography of New Zealand freshwater fishes. *Ital J Zool* 65(Suppl S):73–85
- McDowall RM (1999) Diadromy and genetic diversity in Nearctic and Palearctic fishes. *Mol Ecol* 8:527–528
- McDowall RM (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J Biogeogr* 29:207–220
- McDowall RM (2003) Hawaiian biogeography and the islands' freshwater fish fauna. *J Biogeogr* 30:703–710
- McDowall RM (2004) What biogeography is: a place for process. *J Biogeogr* 31:345–351
- McDowall RM (2005) Biogeography of the Falkland Islands: converging trajectories in the South Atlantic. *J Biogeogr* 32:49–62
- McDowall RM (2007) Hawaiian stream fishes: the role of amphidromy in history, ecology and conservation biology. In: Evenhuis NL and Fitzsimons JM (eds). *Biology of Hawaiian streams and estuaries*. Bish Mus Bull Cult Environ Stud 3:3–9
- McDowall RM (2008) Why are so many boreal freshwater fishes anadromous? Confronting 'conventional wisdom'. *Fish Fisher* 9:1–6
- McGlone MS (2006) Becoming New Zealanders: immigration and the formation of the biota. In: Allen RB, Lee WG (eds) *Biological invasions in New Zealand: analysis and synthesis*. Springer, Heidelberg, Germany, pp 17–32
- Okada Y (1960) Studies on the freshwater fishes of Japan. Prefectural University of Mie, Tsu, 860 pp
- Page RDM (1989) New Zealand and the new biogeography. *N Z J Zool* 16:471–484
- Pole M (1994) The New Zealand flora: entirely long-distance dispersal? *J Biogeogr* 21:625–635
- Pole M (2001) Can long-distance dispersal be inferred from the New Zealand plant fossil record? *Aust J Bot* 49:357–366
- Price JP, Wagner WL (2005) Speciation in Hawaiian angiosperm lineages: cause, consequence and mode. *Evolution* 58:2185–2200
- Radtke RL, Kinzie RA (1991) Hawaiian amphidromous gobies: perspectives on recruitment processes and life history events. In: *New directions in research, management and conservation of Hawaiian freshwater stream ecosystems: proceedings of the 1990 symposium on freshwater*

- stream biology and fisheries management. Division of Aquatic Resources, Department of Land and Natural Resources, Honolulu, HA, USA, pp 125–141
- Ricklefs RA, Schluter D (1993) Species diversity: regional and historical influences. In: Ricklefs RA, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, IL, pp 350–363
- Riddle BR (2005) Is biogeography emerging from its identity crisis? *J Biogeogr* 32:185–186
- Shepherd LD, de Lange PJ, Perrie LR (2009) Multiple colonizations of a remote oceanic archipelago by one species: how common is long-distance dispersal? *J Biogeogr* 36:1972–1977
- Sherman CDH, Hunt A, Ayre DJ (2008) Is life history a barrier to dispersal? Contrasting patterns of genetic differentiation along an oceanographically complex coast. *Biol J Linn Soc* 95:106–116
- Smith PJ, McVeagh SM, Allibone R (2005) Extensive genetic differentiation in *Gobiomorphus breviceps* from New Zealand. *J Fish Biol* 67:627–639
- Stevens MI, Hicks BJ (2009) Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evol Ecol Res* 11:109–123
- Thacker CE, Unmack PJ, Matsui L, Duong P, Huang E (2008) Phylogeography of *Philypnodon* species (Teleostei: Eleotridae) across south-eastern Australia: testing patterns of connectivity across drainage divides and among coastal rivers. *Biol J Linn Soc* 95:175–192
- Thornton IWB (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island Motmot, in its caldera lake. 1. General introduction. *J Biogeogr* 28:1299–1310
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25:1–45
- Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. *J Biogeogr* 34:1–6
- Unmack PJ (2009) Comparative phylogeography of Australian freshwater fishes. In: Biogeography and biodiversity: Book of abstracts: 8th Indo-Pacific Fish Conference and 2009 AFSB Workshop and Conference, Fremantle, Western Australia 31 May–5 June 2009, p. A385
- Wagner WL, Funk VA, eds (1995) Hawaiian biogeography: evolution on a hot-spot archipelago. Smithsonian Institution Press, Washington, DC, 467 pp
- Wallace AR (1880) Island life: or the phenomena and cases of insular faunas and floras including a revision and attempted solution of the problem of geological climates. McMillan, London, 526 pp
- Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small planet *Mol Ecol* 18:3548–3580
- Waters JM, Craw D (2006) Goodbye Gondwana: New Zealand biogeography and the problem of circularity. *Syst Biol* 55:351–356
- Waters JM, Craw D (2008) Evolution and biogeography of New Zealand's longjaw galaxiids (Osmeriformes: Galaxiidae): the genetic effects of glaciation and mountain building. *Freshwater Biol* 53:521–534
- Waters JM, Wallis GP (2001) Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *J Fish Biol* 58:1166–1180
- Waters JM, Allibone RM, Wallis GP (2006) Geological subsidence, river capture and cladogenesis of galaxiid lineages in central New Zealand. *Biol J Linn Soc* 88:367–376
- Wilkinson DM (2003) Dispersal, cladistics and the nature of biogeography. *J Biogeogr* 30:1779–1780
- Winkworth RC, Robertson AW, Ehrendorfer F, Lockhart PJ (1999) The importance of dispersal and recent speciation in the flora of New Zealand. *J Biogeogr* 26:1323–1325
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organ Div Evol* 5:237–247
- Wolf PG, Schneider RTA (2001) Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *J Biogeogr* 28:263–270

- Zink RM (1991) Genetic variation within and between populations of *Lentipes concolor* from Hawaii and Kauai. In: New directions in research, management and conservation of Hawaiian freshwater stream ecosystems: proceedings of the 1990 symposium on freshwater stream biology and fisheries management. Honolulu, Division of Aquatic Resources, Department of Land and Natural Resources, HA, USA, pp 96–105
- Zink RM, Fitzsimons JM, Dittman DL, Reynolds DR, Nishimoto RT (1996) Evolutionary genetics of Hawaiian freshwater fish. *Copeia* 1996:330–335

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