


special issue:

# Feathers to Fur

The ecological transformation of Aotearoa/New Zealand



## Historical and ecological context, pattern and process, in the derivation of New Zealand's freshwater fish fauna

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**Abstract:** This paper explores distribution patterns exhibited by New Zealand's freshwater fish fauna, both fossil and extant, and seeks to clarify processes that have generated these patterns. Knowledge of a Miocene New Zealand terrestrial/freshwater fossil fauna is based substantially on lacustrine deposits in Central Otago. It reflects an ecologically very different fauna from that known today. Nothing is known of the Miocene fluvial fauna. Present-day patterns of distribution and diversity reflect a deep ecological dichotomy. About half the fauna is diadromous, and the habit of these species, of moving to and from the sea, provides them with great resilience in the face of major known landscape perturbations resulting from orogeny and land submergence, glaciation and volcanism. The diadromous species tend to be widespread throughout New Zealand. In contrast, non-diadromous species are more strictly confined to freshwater habitats, and a major means of spread relates to changes in directions and connections of stream flows. As a result, species are much less resilient, they exhibit complex patterns of sympatry, and their ranges are much more localised. Despite all elements in the fauna living across the same landscape in space and time, distribution patterns of the varying species groups display great differences in pattern.

**Keywords:** biogeography; diadromy; Eleotridae; fossil fauna; Galaxiidae; Gondwana; Miocene; resilience

### Introduction

One of the key elements in understanding the history and derivation of a fauna is to distinguish the roles of history and proximate ecology (Endler 1982). This is no surprise, given that all history has an ecological component and that the outcomes of ecological processes form the basis for history. The complex interweaving of history and ecology means that the so-called history/ecology dichotomy does not exist (May 1986), and yet, to understand pattern, whether geographical or phylogenetic, we need to distinguish between the two. In practice, what tends to happen is that ecology is relegated to recent/proximate events and processes, and doesn't become a part of historical analyses, even though there is no escaping the fact that historical pattern is little more than accumulation of the outcomes of past processes or events that are rooted in ecology. I think that New Zealand's freshwater fish fauna is especially amenable to partially separating these two aspects of natural history, as outlined below.

### The place of Gondwana

If we want to understand pattern and process in the New Zealand fauna or flora, we have to begin with a recognition that

the biota has some Gondwanan aspects. I am not as ready as some to say "goodbye" to Gondwana and to attribute the entire biota to dispersal derivations (McGlone 2005, and see Wallis & Trewick 2009). This might seem surprising for a life-long dispersalist (McDowall 1964, 2002), but a strong emphasis on the role of dispersal does not mean that there is no role for Gondwanan vicariance in the origins and derivations of the biota. Rather, it becomes a question of balance and scale (McDowall 1978), and here I argue there is probably still a Gondwanan element in the freshwater fish fauna.

### Miocene submergence

It has been argued that the entire present New Zealand land surface emerged from a previous complete marine inundation in the Oligocene (Campbell 2007; Campbell & Hutching 2007; Landis et al. 2008), which would, of course, mean that the entire terrestrial biota has dispersal origins. However, I contend that some taxa present in New Zealand tell us that some land was present here continuously since proto-New Zealand ("Zealandia": Adams et al. 2009; Tennyson 2010), became detached from Gondwana in the late Cretaceous. However, we have to avoid the circularity trap (McDowall 1973; Waters & Craw 2006) of concluding that there must have been land here because certain biotic elements needed such land connections, and that this is proof of those land connections (Michaux &

Leschen 2005). Geological conclusions need to be supported by geological evidence (McDowall 1973, 2008).

When I say that there are Gondwanan elements, I am not alluding primarily to the biotic elements that most might choose – the usually-touted ‘Flemingian palaeoendemics’ (Fleming 1979), such as tuatara, leiopelmid frogs, mystacinid bats, ratites, and *Nothofagus* beech forests, that are often thought to reflect that ancient Gondwanan connection. Some, such as *Nothofagus* and the ratites, are increasingly being shown to have distributions at least in part influenced by dispersal (Cooper et al. 1992; Haddrath & Baker 2001; Swenson et al. 2001; Knapp et al. 2005; Tennyson 2010). Instead, I am referring to freshwater organisms like the mussel *Echyridella* that has a parasitic life stage that attaches to a freshwater fish, and the freshwater crayfish (*Paranephrops* spp) and its temnocephalid commensal. Such parasitisms or commensalisms make for some complexity if we are to postulate transoceanic dispersal, or even to argue for dispersal to New Zealand down a chain of islands along the Norfolk Ridge (McLoughlin 2001). Dispersals of such groups rather transcend the ostensibly simpler issues of how a few members of a species might have reached New Zealand. These taxa raise the dispersal stakes substantially. Gibbs (2006) nominated the scorpionfly (*Nannochorista*) as a remnant Gondwanan element in the fauna. Wilson (2008) has pointed to phreatoicid freshwater isopods that are substantially hypogean. Triclad turbellarians are another little-mentioned group, as also are oligochaete earthworms that may well have Gondwanan origins and distributions, and there are others – and note that these are mostly animals. There has been a growing tendency for dispersal explanations for much of the flora that might once have been included as Gondwanan relicts (Lee et al. 2001; McGlone 2005, 2006; reviewed in McDowall 2008; Wallis & Trewick 2009). Some of the often-cited palaeoendemics, such as *Nothofagus*, can now in part be discounted based on evidence that dates the separation of disjunct stocks across broad sea gaps (Swenson et al. 2001; Knapp et al. 2005), though others have pointed to a likelihood that *Agathis*, for example, has been here since there were Gondwanan connections (Stockler et al. 2002). In a way, this is a digression, as many of Fleming’s palaeoendemics seem to be taxa that have ‘hung on’ here and nowhere else, but were probably once much more widespread (McDowall 2008).

### Gondwana and the freshwater fish fauna

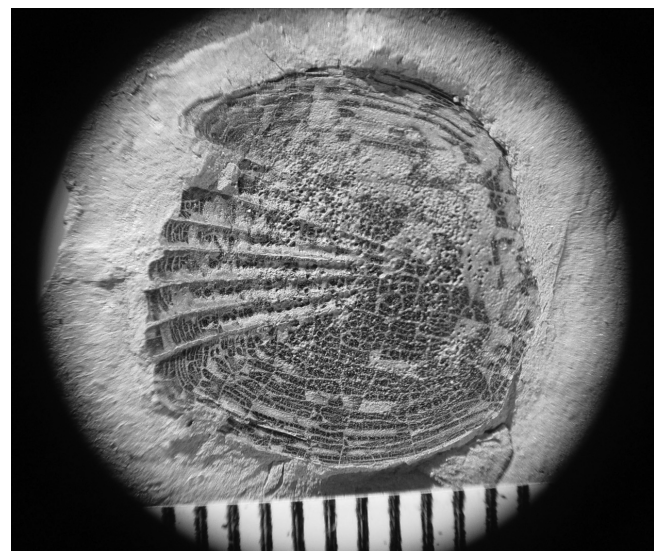
It is possible that there was an ancient role for Gondwana in the freshwater fish fauna, though it has limited implications for the contemporary fauna. There is every reason to think that there would have been freshwater fish of some sort on Gondwana, and some of them could have come with proto-New Zealand as it moved off into the Cretaceous forerunner of the Pacific Ocean. We don’t know how important a Gondwanan source for the fauna was, but I have no doubt that it was minor in the context of today’s fauna, most elements of which arrived in New Zealand by transoceanic dispersal (McDowall 1990, 2002, 2008). However, a few elements in the freshwater fish fauna may reflect ancient Gondwanan origins, e.g. perhaps the species of the non-diadromous ‘pencil galaxias’ complex (a group of small, sub-alpine species; McDowall 2002). These may have quite ancient relationships that lie beyond the New Zealand region, although this question is yet to be explored in detail, and the relationships remain obscure.

### Miocene and Pleistocene freshwater fish fossils

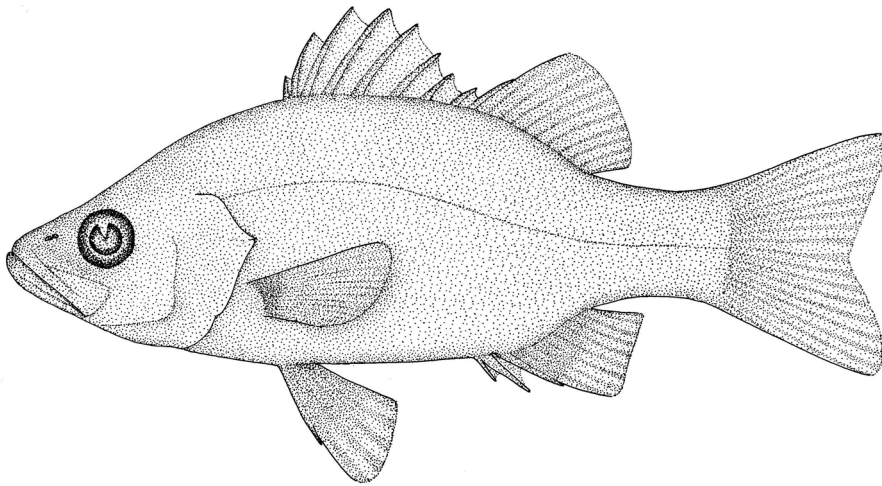
Information on a freshwater fish fauna that was presumably

present here from early post-Oligocene times is relatively sparse, although recent fossil studies have been revealing. The Miocene fossil fauna contained some highly distinct elements, when compared with the extant fauna (McDowall & Pole 1997; McDowall & Lee 2005; McDowall et al. 2006b; Lee et al. 2007). However, the ancient fossil fauna, presently being discovered, was ecologically very different from the extant fauna. All fossils discovered so far are lacustrine in origin, whereas the modern fauna includes very little that is distinctively lacustrine. In general, New Zealand’s significant lakes are very young (Lowe & Green 1992), mostly post-glacial and/or profoundly influenced (probably cleared of all fauna) by quite recent volcanism, so that scope for survival to the present of ancient lacustrine freshwater fish elements is limited. There is scarcely any lake location now in existence where fishes could have survived through to the present from the mid- or even later-Cenozoic. A lacustrine endemic galaxiid in some small Northland lakes (e.g. *Galaxias gracilis* in the Poutu Lakes on the north head of Kaipara Harbour) may reflect the fact that these lakes are pre-glacial (Rowe & Chisnall 1997). However, these lakes are scarcely old in geological terms, relative to survival from the Miocene period when many of the known fish fossils were alive, and they tell us little about a more ancient fauna. Rather, extant lacustrine faunas are mostly either diadromous and need access to and from the sea, or are derived directly by loss of diadromy at the population scale, as is often true today, in species like koaro (*Galaxias brevipinnis*), or common bully (*Gobiomorphus cotidianus*; McDowall 1990). Bearing in mind this contrast between the known ancient lacustrine fossil fauna and the contemporary, largely fluvial, elements, the fossil fauna nevertheless has interesting features.

Some Miocene fossil scales (Fig. 1) indicate presence of a family of fishes for which we have no other reported hint. Though only 1½ of these scales have been recovered, they show that in Miocene Palaeo-lake Manuherikia there was a likely relative of the Australian percichthyid cods and basses (family Percichthyidae; Fig. 2), of which we have no other trace (McDowall & Lee 2005) – unless disarticulated fish bones found around St Bathans by Trevor Worthy (pers.



**Figure 1.** Scale of a fish from a Miocene deposit at Bannockburn, Central Otago, probably from a percichthyid, and not otherwise known from New Zealand fresh waters (scale millimetres; photo D.E. Lee).



**Figure 2.** The Australian estuary perch (*Macquaria colonorum*; f. Percichthyidae), perhaps something like a fish species once present in Palaeo-lake Manuherikia, in Central Otago, in the Miocene.

comm.) include elements from fish of this type. As well, diverse galaxiid fishes are present in Miocene lake deposits in Central Otago, galaxiids that were different from anything present in the fauna now (McDowall & Pole 1997; Lee et al. 2007).

Amongst the known Miocene lake fauna were also probable representatives of the modern bullies (family Eleotridae, genus *Gobiomorphus*) (McDowall et al. 2006b). I previously have considered bullies to be relatively recent members of the fauna, but we now know that they were already represented in the mid Cenozoic, and our *Gobiomorphus* fossils are perhaps the oldest eleotrid fossils known. A few, much more recent, eleotrid fossils are also known from Pleistocene lake deposits inland from Gisborne (McDowall et al. 2006b).

A Pleistocene fossil of the now-extinct grayling (*Prototroctes* sp.; McDowall et al. 2006a) was also an interesting find, but tells us little that is new.

The contrast between this emerging mid-Tertiary lacustrine fauna and the contemporary fluvial fauna is misleading, because there was almost certainly a fluvial fauna here in the mid-Tertiary about which we know nothing. Even though the Miocene New Zealand landscape was regarded as probably of low relief, there must have been rivers here, though they were perhaps unlike those of today with their steep gradients, swift flows and coarse, gravelly substrates. Thus, all we can say with certainty is that the known Miocene freshwater fish fauna was probably very different from what is present today: little or none of the known Miocene lacustrine fauna is still here, as far as we can tell, so the turnover of the lacustrine fauna is virtually complete. Phylogenetic connections between the Miocene and Recent fish faunas are, at best, uncertain.

### The place of extinction

We don't know whether the Miocene eleotrids were distinct from Recent forms, but we should probably assume that they were, though they may have resembled the extant *Gobiomorphus cotidianus*, which is common around the shores of many modern lakes. It is possible that some of the contemporary fluvial fish species are derived from former lacustrine taxa, though nothing that is currently known hints of this, and we will probably never know with any assurance.

Thus, our limited fossil fauna does not take us very far in our attempts to explore pattern and process through Cenozoic history, especially given the lacustrine/fluvial dichotomy, outlined above. Instead, we need to develop ideas about the role of history for the fauna through an examination of contemporary distribution patterns, particularly where there is

scope for exploring patterns in both distribution and genetics in relation to earth history.

### External origins of the fauna

Almost certainly there has been a continual process of augmentation of the fish fauna through the Cenozoic by invasion of New Zealand fresh waters by arrivals from across the sea – probably from Australia and Tasmania. Judging by what is known of the contemporary phylogenetic relationships of the fauna, there were at least 10, perhaps more, different historical invasion events, with arrival of a lamprey, at least two anguillid eels, a smelt, a grayling, at least four galaxiids and at least one eleotrid bully (McDowall 1990, 2002, 2008). In theory, some of the elements shared with Australia could have originated in New Zealand and have spread northwest to Australia, though ocean currents probably always favoured a western origin and eastwards dispersal. We have little idea of the historical timing of most of these events, though molecular studies may provide estimates of when dispersal took place, or at least may allow us to date the most recent gene flow. Waters et al. (2000) attempted this for one widespread galaxiid, as did Waters and McDowall (2005) for the galaxiid genus *Neochanna*. Both studies point to Miocene–Pliocene connections, but the dates of any dispersal events were vague.

In addition, there are at least two instances in which members of the contemporary freshwater fish fauna were derived from marine species in the seas around New Zealand; the torrentfish (*Cheimarrichthys fosteri*) and black flounder (*Rhombosolea retiaria*) probably have their nearest relatives in New Zealand's coastal seas (McDowall 1990).

Invasion events persist well into current history, as with the Australian spotted eel (*Anguilla reinhardtii*), which came to New Zealand in the 1980s (McDowall et al. 1998). However, there are unauthenticated hints of an earlier arrival (Phillipps 1925), and we may be looking at repeated, episodic arrivals of this species across time. In addition, two small gobies (belonging to the genera *Parioglossus* and *Gobiopterus*) have been recognised in our fresh waters in very recent times (McDowall 2001; McDowall & David 2008). However, we cannot determine whether these gobies have actually long been here undiscovered, or came here recently, as has been explored for contemporary arrivals of marine fish species by Francis and Evans (1993) and Francis et al. (1999). Furthermore, if their arrivals are recent, we do not know whether the gobies came as a result of natural dispersal events, or had anthropogenic drivers (probably involving transport in ships' ballast water).



## The place of diadromy

There is a deep ecological dichotomy in the fauna that we have to understand to make sense of pattern. About half the species in the fauna (18 of 39) are diadromous (Table 1), in which there are dual regular migrations between marine and freshwater environments in the life of each individual fish (McDowall 1988). These inter-biome migrations vary in their directions, seasonality, and the life history stages that undertake the movements, although from the broad perspective of both historical and ecological biogeography these variations are not important. What is critically important is to recognise that at some stage, sometimes for many months, these ostensibly freshwater fishes are living at sea. The presence of diadromy provides a distinctive and important perspective on mechanisms that drive distribution patterns of New Zealand's freshwater fishes, in a way that was not recognised by most early workers. However, the role of life at sea for these species was identified by Charles Darwin (1873) as early as the 1870s and by British ichthyologist George Boulenger in the early 1900s (Boulenger 1902). More recently, there has been increased recognition of the number and diversity of species in which diadromous life cycles are known (McDowall 1964, 1988, 1990, 2002). An important secondary process of diversification relates to a loss of diadromy, and establishment of more localised, non-diadromous lineages across the New Zealand landscape (McDowall 1990; Waters & Wallis 2001) and this shift has undoubtedly importance in the evolutionary history of the fauna.

### Diadromy and derivations of the fauna

The ability to live at sea has important implications across broad, geological time scales. Diadromy is probably ancestral in some groups, such as lampreys, anguillid eels, and also the primitive lower euteleostean fishes, a group that includes galaxiids and retropinnids (McDowall 1997). I have long argued (McDowall 1964) that derivations of much of the freshwater fish fauna result from post-Gondwanan, transoceanic dispersal, as discussed above. Five species in three families in the contemporary fauna (Geotriidae, Anguillidae, Galaxiidae) are known to occur also in south-eastern Australia (Table 1), and two of them are in Patagonian South America as well. What is known of their genetics suggests that there has been gene flow between south-eastern Australian and New Zealand populations far more recently than implied by a Gondwanan vicariance scenario (Waters & Burridge 1999; Waters et al. 2000; Gill et

al. 2003). Moreover, in every family represented in the fauna, some or all species are diadromous (Table 1). And the process of dispersion to New Zealand from elsewhere continues into the present, with the recent arrival of the Australian spotted eel, as already mentioned. The role of biotic dispersal to New Zealand is becoming increasingly accepted, especially for the New Zealand flora (McGlone 2005; Gibbs 2006), and has always, in my view, applied to the freshwater fish fauna (McDowall 1964, 1978). Moreover, the growing crescendo of claims for the complete submergence of the entire New Zealand landscape in the Oligocene (Campbell & Hutching 2007; Landis et al. 2008) imply that the entire biota reached New Zealand across the sea since the Oligocene. However important this conclusion might be for the biota of New Zealand as a whole, it makes little difference to the freshwater fish fauna since there seems little impediment to post-Oligocene dispersal of marine life stages across the sea.

### Diadromy and proximate patterns of distribution

There is a fundamental dichotomy that is applicable to the distributions (as opposed to the derivations) of the freshwater fish fauna across the New Zealand landscape that also relates to whether or not species are diadromous. This has explicit and important implications for explaining some details of contemporary distribution patterns.

Diadromous species, with few exceptions, have distributions that span the full latitudinal range of New Zealand (McDowall 1998), so that the southern fauna is much the same, taxonomically, as the northern one. There is virtually no latitudinal shift in species diversity or change in species composition of diadromous components of the fauna, from north to south. These diadromous species exhibit distribution patterns that do not reflect any of New Zealand's late Cenozoic geomorphologic history. There are no residual impacts from: (1) uplift of the Southern Alps; (2) Pliocene submergence of the southern North Island; (3) Pleistocene glaciation; or (4) Recent volcanism; all of which are bound to have had serious adverse impacts on freshwater habitats. Resilience and/or recovery of the diadromous fauna following all sorts of perturbations have been very strong. The present distribution patterns of diadromous species are as if none of these geomorphic events had ever happened.

There must have been contemporaneous historic impacts on the freshwater fauna resulting from glaciation in the western South Island, when glacial ice sheets that extended beyond existing sea levels along part of the West Coast would have obliterated the river fauna (Main 1989). Similarly, volcanism would certainly have removed fauna from rivers in areas of major ash deposition, across the central North Island (McDowall 1996) and to the north east. The impact would have been felt in all rivers draining the ash deposition area and have extended, during floods, well beyond the deposition zone, when ash would have been flushed downstream and into the sea. At lesser spatial scales, impacts probably resulted from eruption of Mt. Taranaki only about 300 years ago (Neall 1992), and of Mt Tarawera in 1886. But the ability of diadromous species to reinvade seriously perturbed habitats once those habitats again became congenial to fish life, has meant that populations of diadromous species were probably soon restored by invasion from coastal seas.

There are, however, limits on the inland penetration of river systems by diadromous species that depend on topography, explicit barriers to migration, and the migratory aptitudes and instincts of the diadromous species. In this regard, there

**Table 1.** Composition of the New Zealand freshwater fish fauna (numbers of currently recognised species).

Family	No. species diadromous	No. species non-diadromous	No. species also present beyond New Zealand
Geotriidae	1	0	1
Anguillidae	3	0	2
Retropinnidae	3	0	0
Galaxiidae	5	18*	3
Eleotriidae	4	3*	0
Pinguipedidae	1	0	0
Pleuronectidae	1	0	0

\* probably includes unrecognised taxonomic diversity, and number of species may increase after further taxonomic study

is a broad, behaviour-driven continuum, from species that scarcely penetrate beyond river estuaries, to others that penetrate hundreds of kilometres inland. Inland penetration is substantial, enhanced in some species that can climb steep waterfalls, mostly as juveniles (McDowall 1990).

Thus, for diadromous species, which make up about half the fauna (Table 1), there is no hint of historical change in the fauna across any time scale. Rather, these fish species exhibit high resilience to perturbation and there has clearly been continual, rapid restoration of fish communities following adverse impacts once congenial habitats have been restored, just as happens today when there are local fish kills that result from industrial discharges of toxic materials or from ash falls and lahars etc. from the central North Island volcanoes (Sheppard 1996; Dedual & Cudby 1999; Manville 2002).

### Implications of not being diadromous

The scenario is very different for the non-diadromous half of the fauna (Table 1). Non-diadromous species have much more restricted latitudinal ranges and there is a major shift in taxonomic composition across latitudes, so that the northern fauna is entirely different from the southern one. As well, in virtually every taxonomic group, molecular studies are revealing increasing levels of taxonomic diversity in non-diadromous species groups and lineages (Waters & Wallis 2001; Smith et al. 2005), so that patterns of distribution may be even more fragmented and more localised than the present taxonomy indicates (McDowall 1990). Perhaps, as a consequence, it is in this group that the negative impacts of introduced trout have been most obvious (McDowall 1968, 2006b; McIntosh et al. 2010).

Moreover, geographical patterns in the non-diadromous fauna reflect impacts of ancient to recent, geomorphologic, volcanic, and climatic history; broad-scale events like the following.

#### (1) Connections across sea straits

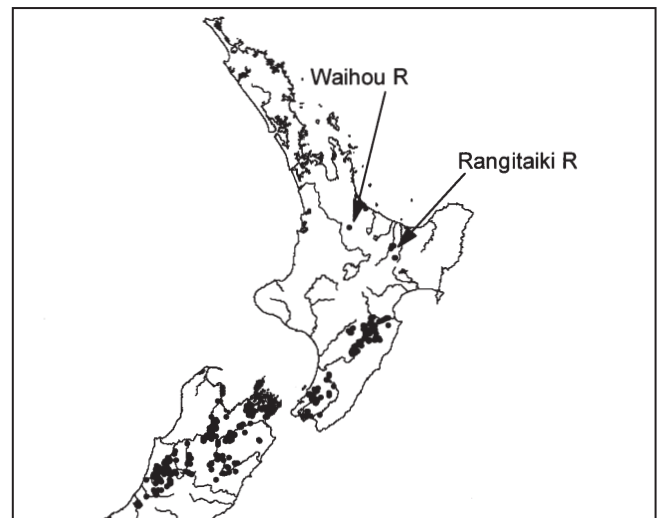
Some species, such as dwarf galaxias (*Galaxias divergens*; Fig. 3), brown mudfish (*Neochanna apoda*), and upland bully (*Gobiomorphus breviceps*), have distributions that span Cook Strait, and Gollum galaxias (*Galaxias gollumoides*; Fig. 4), *Galaxias* 'southern', and upland bully, span Foveaux Strait. These distributions reflect the presence of land bridges across these straits as recently as the Pleistocene (Fleming 1979). Other taxa, however, had distributions that seem limited by the straits, as with Cran's bully (*Gobiomorphus basalis*) in the North Island or alpine galaxias (*Galaxias paucispondylus*) in the South Island; both reach close to Cook Strait, but neither crosses it. This may be due to the alpine galaxias needing low temperatures, excluding it from using low-elevation connections between the North and South Islands, but that is not true of Cran's bully, which is widespread at low elevations in northern New Zealand.

#### (2) Central North Island volcanism

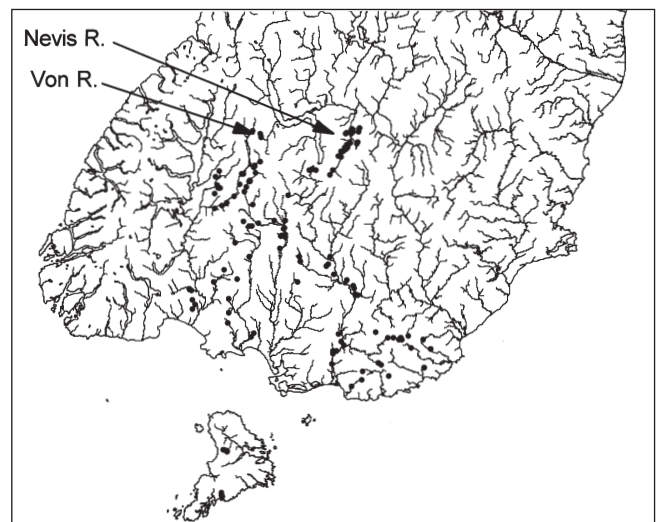
This has resulted in broad absences in the central and north-eastern North Island of non-diadromous species, such as dwarf galaxias (Fig. 3) and Cran's bully, which are present in contiguous areas to both north and south (McDowall 1996).

#### (3) Uplift of the Southern Alps

Uplift of the Southern Alps has been associated with divergence of stocks north-west and south-east of the rising mountain chains, as in brown and Canterbury mudfish, and genetically



**Figure 3.** The dwarf galaxias (*Galaxias divergens*) is widespread across central New Zealand on both sides of Cook Strait. The disjunct distributions of two northern outliers in the Waihou and Rangitaiki rivers probably relate to extirpation of populations in the central North Island by Taupo volcanism.

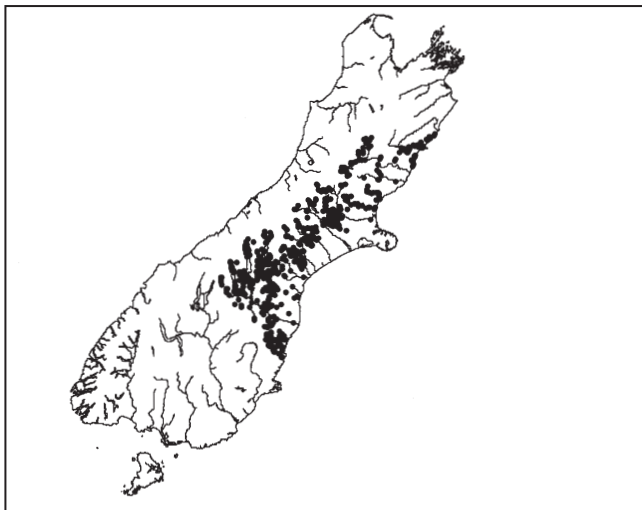


**Figure 4.** The Southland roundhead galaxias (*Galaxias gollumoides*) is widespread in the rivers of the Southland Plains, but also found in two tributaries of the Clutha River (Von and Nevis) as a result of headwater tributaries of Southland rivers being captured and their flows redirected north into the Clutha.

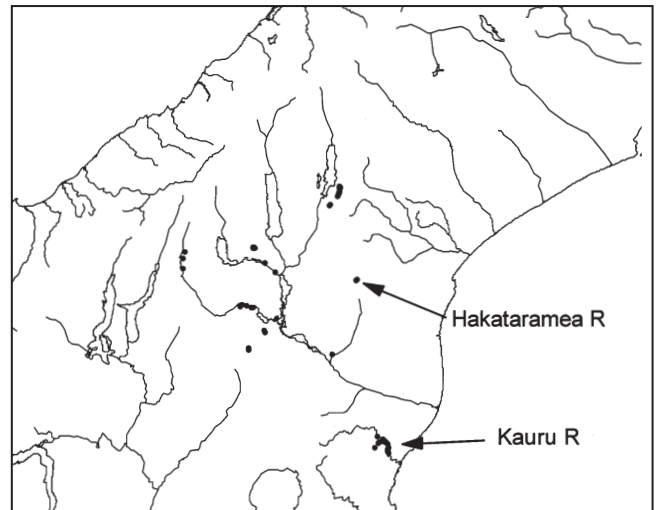
divergent stocks of upland bully (Smith et al. 2005; Stevens & Hicks 2009) that may represent hitherto unrecognised taxonomic diversity.

#### (4) Glaciation

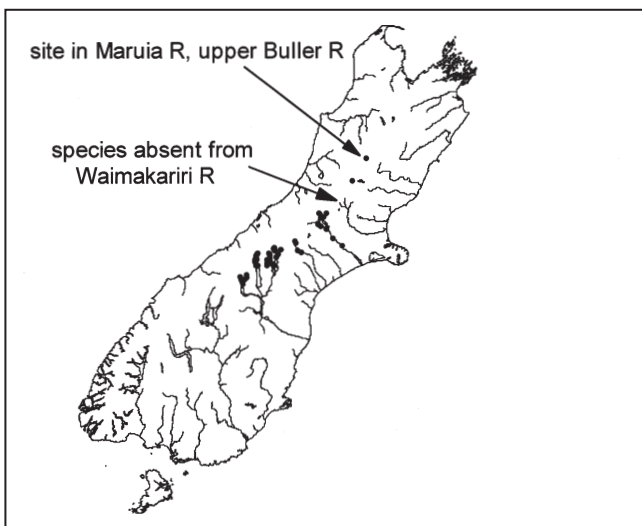
Glaciation has led to loss and subsequent lack of recovery of non-diadromous species, such as dwarf galaxias, brown mudfish and upland bully in the central western South Island, the 'beech gap' (Main 1989; Treweek & Wallis 2001). Less obvious is the certainty that at times of Pleistocene glacial advances, freshwater fishes would have been driven to lower elevations from the inter-montane valleys of the eastern Southern Alps, and it seems that cold-loving species, like Canterbury galaxias (*G. vulgaris*; Fig. 5) alpine galaxias, and



**Figure 5.** The Canterbury galaxias (*Galaxias vulgaris*) would have been driven from the inter-montane valleys of the eastern Southern Alps by glacial advance, but has reinvaded (as shown) following glacial retreat.



**Figure 7.** The lowland longjaw galaxias (*Galaxias cobitinis*) is widespread in the Mackenzie Basin, with an outlier in the Kauru River, a lower Kakanui River tributary, where it probably survives in upwelling, cold groundwater.



**Figure 6.** The upland longjaw galaxias (*Galaxias prognathus*) would have been driven by glacial advance from the inter-montane valleys, and has reinvaded most of them (Hurunui, Rakaia, Rangitata, Waitaki), but has failed to do so in the Waimakariri River, for unknown reasons. An outlier in the upper Maruia is a probable consequence of headwater capture by the Buller River.

upland longjaw galaxias (*G. prognathus*; Fig. 6) have been successful in re-occupying these high elevation valleys once glacial ice retreated. Interestingly, upland longjaws seem to have not reoccupied the Waimakariri River (Fig. 6), whereas Canterbury galaxias (Fig. 5), alpine galaxias and upland bully have all done so. Looking a little more broadly, taxonomically, freshwater crayfish (*Paranephrops* spp) seem also to have been unable to (re)occupy the inter-montane valleys since glacial retreat (McDowall 2005).

**(5) Post-glacial temperature elevation**

Part of the story of the hypothesised shift of these cold-loving species upstream into the inter-montane valleys may well have been that they were driven upstream from lower elevation rivers by elevated post-glacial temperatures. In this regard, survival of a few low-elevation relicts of lowland longjaw galaxias (*G. cobitinis*), as in the Kauru River, a tributary of the Kakanui

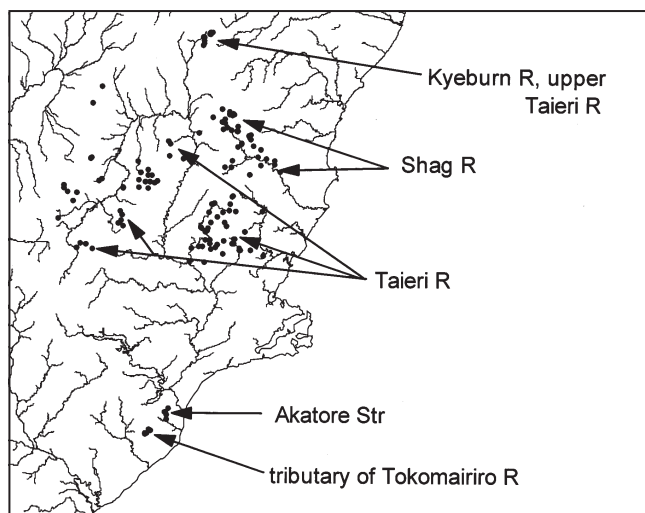
River, inland from Oamaru, and in the upper Hakataramea River (Fig. 7), is distinctive. Persistence in the Kauru River may have been possible only because of localised sites of cold, upwelling groundwater (McDowall & Waters 2002).

A series of other distribution patterns begin to make sense once we know something of the broader geological and climatic history of New Zealand. There has, for instance, been speciation that has resulted in generation of localised endemics, most evident in the central and southern South Island (Waters et al. 2001; McDowall & Waters 2002, 2003; McDowall 2006a). Molecular evidence suggests that *Galaxias* ‘northern’ and Canterbury galaxias spread north from Otago, across the formative Canterbury Plains (Waters & Wallis 2001), presumably as the plains were formed by outwash from the big, rapidly-eroding, inter-montane valleys of the eastern Southern Alps.

**(6) Changing fluvial connections**

In some instances, very local events like headwater stream captures, have resulted in elements characteristic of one region gaining a foothold in neighbouring regions. An example is the presence of upland longjaw galaxias west of the Southern Alps in the vicinity of the Lewis Pass (Maruia River, a headwater tributary of the west-flowing Buller River; Fig. 6). Also, species such as Gollum galaxias and *Galaxias* ‘southern’ that are otherwise known only from the Southland Plains and Stewart Island, are found in southern tributaries of the east-flowing Clutha River (Nevis and/or Von Rivers; Waters et al. 2001; McDowall 2006a), as a result of small headwater capture events (Fig. 4). There are complex patterns of galaxiid distributions in the Pelorus and Wairau Rivers in Marlborough that also reflect river capture events (Craw et al. 2007b). Populations of alpine galaxias in headwaters of the Manuherikia River (Clutha River system, Otago) may be an outcome of former connections between upper reaches of that river and the Ahuriri, a major southern inland tributary of the Waitaki River to the north. Also alpine galaxias in the Lochy River, which now flows into the southern arm of Lake Wakatipu (which itself now drains east into the Clutha via the Kawarau River), may reflect that this arm of the lake formerly flowed south into the Matura River, where alpine galaxias is also present. The Lochy and Manuherikia populations are the





**Figure 8.** The geographical range of Taieri flathead galaxias (*Galaxias depressiceps*) with two unpredictable outliers in Akatore Stream and in the Narrowdale, a tributary of the Tokomairiro River in coastal South Otago.

only instances of this species in the entire Clutha catchment, and both may reflect former fluvial connections, rather than present ones. Other similar instances are explored by Craw et al. (2007a).

Some distribution patterns may have been influenced in human time scales by establishment of novel fluvial connections that resulted from construction of water races by 19<sup>th</sup> century gold miners, as in Totara Creek, an upper tributary of the Taieri River in the Maniototo, Otago (Allibone 2000), and perhaps also some stocks of the *G. vulgaris* species complex in upper reaches of the Shag River, a coastal drainage in North Otago (Fig. 8). So, these are localised, recent, anthropogenic manifestations of the same types of processes as have occurred naturally over longer time scales.

#### (7) Enigmatic distribution patterns indicated by molecular evidence

Some speciation processes are understood in a phylogenetic sense on the basis of molecular and morphological evidence, but are not understood in a geographical sense, in that we do not know how allopatries developed, or even whether allopatry was involved in speciation. Nevertheless, non-diadromous species groups often exhibit within-group allopatries across their ranges (though not entirely). If radiation was driven by allopatry, there has clearly been some redistribution, following divergence and reproductive isolation, which has created areas of marginal (parapatry) or even broad-scale, geographical overlap (sympatry). Similarly, some distribution patterns seem biogeographically inexplicable, as, for example, disjunct populations of Taieri flathead galaxias (*G. depressiceps*) in Akatore Creek and in the Narrowdale, part of the Tokomairiro River, both small, independent coastal catchments near the mouth of the Taieri River (Fig. 8). Highly disjunct populations of dwarf galaxias in tributaries of the Waihou River, in the Hauraki Plains and the upper Rangitaiki River in inland Bay of Plenty, seem likely to be northern relicts of a formerly widespread species, still widely present in the southern North Island and south into the northern South Island, but probably extirpated across the central and north-eastern North Island by Taupo volcanism (Fig. 3) (McDowall 1996).

Upland bully and Cran's bully exhibit a broad zone of overlap in the southern North Island, extending as far north

as Taranaki in the western central North Island. Both species are absent from all but the inland, eastern, streams that drain Mount Taranaki, and this is likely to be a persisting outcome of the mountain's volcanic eruptions, most recently c. 300 years ago (Neall 1992). These two species have presumably regained a presence in these east-flowing tributaries of the inland slopes of the mountain via connections from more remote inland/central North Island river systems that were not adversely affected by the mountain's volcanism.

It seems that the most active local speciation/radiation processes of the non-diadromous fauna took place across the old Otago peneplain, which is widely regarded as the most ancient well-defined land surface in New Zealand: if any of New Zealand was permanently emergent, it was probably the southern half of the South Island, though the enduring emergence of even this area from sea coverage has been questioned (Campbell 2007; Campbell & Hutching 2007; Landis et al. 2008). Moreover, diversification may have involved an area rather wider than just the old Otago peneplain, perhaps extending north into the present Waitaki River. Certainly, there is some local endemism in the freshwater fish fauna of the Mackenzie Basin (bignose galaxias, lowland longjaw galaxias), an area which some consider to have low levels of taxonomic endemism in other groups (Wardle 1968). Connections south into Stewart Island are also implicit, although dispersal across an emergent Foveaux Strait in the Pleistocene may be all that was involved.

Thus, it seems likely that various non-diadromous species complexes evolved, diversified, and spread across the landscape in response to events in New Zealand's earth history, such as uplift of the Southern Alps, land connections across now-existing sea straits, and periodic cycles of submergence and re-emergence of land, such as the Pliocene submergence of the southern North Island. However, patterns of distribution and diversification differ substantially between different species complexes and there is no consistent imprint of earth history in these patterns. There is growing knowledge of the interplay between speciation processes, biogeography and geological history (McDowall 1970; Waters & Wallis 2001; Burrige et al. 2006; Craw et al. 2007a, b; Waters & Craw 2008).

#### Phylogenetic links between diadromous and non-diadromous elements

Phylogenetically, much of the non-diadromous fauna has a diadromous ancestry. In part, the non-diadromous element arose through the abandonment of diadromy, then local speciation events that were facilitated by the reproductive isolation resulting from the loss of diadromy (McDowall 1970, 1990; Waters & Wallis 2001). The extent to which phylogenies reflect single losses of diadromy in the various species groups, followed by radiation, or multiple losses of diadromy and less local radiation, is still uncertain. Nevertheless, derivations of the diadromous fauna are often beyond New Zealand, whereas relationships of most of the non-diadromous species lie among other New Zealand species that often have a diadromous ancestry, such as the *Galaxias vulgaris* species complex (Waters et al. 2001), the genus *Neochanna* (Waters & McDowall 2005), and *Gobiomorphus bullies* (Stevens & Hicks 2009).

#### Conclusions

Taking a broad perspective, much of the ebb and flow of establishment and diversification of the freshwater fish fauna

in New Zealand has been a result of addition from outside (especially Australia), and also a little from New Zealand seas (torrentfish and black flounder). Present distribution patterns within New Zealand reflect great resilience of the diadromous element, though there has been local diversification within the diadromous element in the fauna, as a result of processes that are at present poorly understood.

Much of the diversification, however, has resulted from abandonment of diadromy, and subsequent localised divergence in the allopatry that an entirely freshwater life history facilitates; this protects locally-evolving and adapting populations from continual invasion of other genotypes from elsewhere, via the sea. Thus, contemporary distribution patterns of widespread diadromous species reflect their resilience to local extirpation and their ability to reinvade river systems from the sea. In contrast, non-diadromous species have much more restricted distribution patterns. These reflect enduring effects of local extirpations resulting from a wide variety of environmental perturbations, local speciation processes, and the effects of ongoing geomorphologic changes, that include mountain building, volcanism, glaciation and other climatic changes, and local shifting of fluvial connections across the landscape.

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