Identifying freshwater ecosystems with nationally important natural heritage values: development of a biogeographic framework

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SCIENCE FOR CONSERVATION 274

Published by
Science & Technical Publishing
Department of Conservation
PO Box 10420, The Terrace
Wellington 6143, New Zealand

Cover: Ohinemuri River in Karangahake Gorge, Coromandel.
Photo: John Leathwick.

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
Individual copies are printed, and are also available from the departmental website in pdf form. Titles are listed in our catalogue on the website, refer www.doc.govt.nz under *Publications*, then *Science & technical*.

ISSN 1173-2946
ISBN 978-0-478-14207-5 (hardcopy)
ISBN 978-0-478-14208-2 (web PDF)

This report was prepared for publication by Science & Technical Publishing; editing by Sue Hallas and layout by Lynette Clelland. Publication was approved by the Chief Scientist (Research, Development & Improvement Division), Department of Conservation, Wellington, New Zealand.

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ABSTRACT

This report describes a biogeographic classification for use in identifying water bodies of national importance in New Zealand. The classification aims to identify geographic units likely to have experienced similar physical disturbance regimes, while taking cognisance of potential recolonisation pathways and/or geographic barriers to the dispersal of freshwater biota. The classification is based on: biotic distributions, particularly those of non-diadromous fish (the New Zealand Freshwater Fish Database); genetic similarity between different populations, as determined from molecular analyses; and physical disturbances, particularly the Last Glacial Maximum, volcanic eruptions in the central North Island and seismic activity, especially in mountainous parts of the South Island. Seven biogeographic provinces and 19 units have been defined.

Leathwick, J.R.; Collier, K.; Chadderton, L. 2007: Identifying freshwater ecosystems with nationally important natural heritage values: development of a biogeographic framework. *Science for Conservation 274*. Department of Conservation, Wellington. 30 p.

1. Introduction

1.1 WATER-BODIES OF NATIONAL IMPORTANCE

At the direction of Cabinet, the New Zealand Government is currently developing an integrated approach to the sustainable management of freshwater resources. As part of this project, several government departments have been charged with identifying waters of national importance (WONI) with reference to their value for conservation, recreation, culture and heritage, irrigation, energy generation, industrial use and tourism. The Department of Conservation (DOC) is responsible for the natural heritage component of this process. Its responsibility to assess the conservation value of different water bodies also links strongly to the New Zealand Biodiversity Strategy (Anon. 1998), which identified the need to protect a comprehensive and representative range of freshwater ecosystems.

Identification of nationally-important freshwater ecosystems requires sites to be assessed in a way that accounts for (1) variability among sets of environmental features considered to lead to the development of different aquatic communities (hydroclasses), and (2) variability in biogeographic drivers that influence large-scale biotic pattern, even in the absence of anthropogenic disturbance. Therefore, a classification must discriminate hydroclasses and incorporate a spatial framework to capture biogeographic pattern. A nested approach, whereby sites representing the various hydroclasses are assessed using criteria applied within each biogeographic unit, is required.

To achieve this goal, DOC contracted the National Institute of Water and Atmospheric Research (NIWA) and collaborating agencies to carry out three projects. The first explored relevant background information and proposed a list of criteria that could be used to assess natural heritage values in freshwater and estuarine ecosystems (Collier et al. 2003). In the second project, NIWA staff in Christchurch are developing a classification of New Zealand's freshwater resources using classification techniques applied to a range of environmental variables relevant to the distributions of aquatic biota. This report describes the third project, which is designed to classify New Zealand into a number of biogeographic units based on the likely impacts of historic events such as glaciation and volcanism that have affected the geographic distributions of major freshwater taxa. The environmental and biogeographic frameworks produced by these last two projects will, in turn, be combined with information describing naturalness, anthropogenic pressure and condition to identify a set of nationally important water bodies for biodiversity protection.

1.2 DEVELOPMENT OF A BIOGEOGRAPHIC LAYER

One of the major challenges in developing a biogeographic layer for New Zealand's fresh waters is the relative paucity of distribution data for most freshwater biota, a problem that is exacerbated by the lack of taxonomies for many groups of organisms. Reasonably comprehensive distribution data are available for only a few taxonomic groups, with only those for fish (New Zealand Freshwater Fish

Database: McDowall & Richardson 1983) resulting from systematic sampling that records both species presence and absence. While some other taxonomic groups have been widely sampled, datasets generally record only species presences (e.g. maps of the distributions of mayflies, stoneflies and caddisflies), with no indication of whether absences reflect genuine species absences or simply a lack of sampling. Although extensive sampling of aquatic invertebrate communities has been used as a tool to assess water quality, taxa are frequently not identified beyond the level of genera, and so insufficient data have been assembled in a form that could support national analyses of species distributions, although this process is underway.

Additional information relevant to the development of a biogeographic layer is provided by analyses of genetic differences between groups of related species, and between different populations of the same species. These analyses, in turn, provide an indication of the likelihood of genetic interchange between populations, allowing inferences to be made concerning past geographic linkages between different water bodies, particularly where the information is for species with limited dispersal ability (such as non-diadromous fish and aquatic invertebrates lacking winged adults or other means of long-distance dispersal).

Descriptions of physical disturbances of New Zealand's landscapes are a third source of information that can be used in constructing a biogeographic classification. For example, extensive investigations have been carried out into the nature of environmental changes during the Last Glacial Maximum (Newnham et al. 1999) and the potential impacts of these on terrestrial biota, particularly New Zealand's flora (e.g. Wardle 1963; McGlone 1988), but also aquatic invertebrates (Craig 1969). Numerous studies have also been made of the distributions and ages of extensive rhyolitic tephras deposited across the central North Island during devastating eruptions from the Taupo Volcanic Zone (e.g. Froggatt & Lowe 1990), and the effects of these on biota have been considered for plant communities (Leathwick & Mitchell 1992) and freshwater fish (McDowall 1996). The effects of more long-term geological changes arising from tectonic activity and plate movement have also been suggested as having the potential to affect species distributions (e.g. Fleming 1979). While evidence for such effects on patterns of endemism in vascular plants has been argued for by McGlone (1985), links between current species distributions and broad features of New Zealand's geology have been questioned by Cooper (1989), based on the antiquity of various geological elements (terranes) relative to the average generation time and mobility of most species.

The remainder of this report describes the process and results of using the three types of information described above to develop a classification of New Zealand that delineates areas likely to exhibit similar historical/geographical effects on aquatic species assemblages. In particular, we have attempted to identify units differing not in physical environment or habitat (e.g. as in Harding & Winterbourn 1997; Snelder & Biggs 2002) but, rather, in their history of catastrophic disturbance and re-colonisation. In particular, we differentiate geographic units in which biota are likely to have experienced similar impacts from major disturbances, principally from the Last Glacial Maximum and/or volcanism, while taking account of geographic barriers and/or linkages affecting the ability of surviving taxa to reoccupy their former or potential ranges. Where possible, we attempt to integrate this information with known species patterns.

2. Methods

2.1 BIOLOGICAL DATA

The most comprehensive information describing the distributions of native freshwater biota is for New Zealand's fish species, with many lakes, rivers and streams having been systematically sampled using a variety of techniques including electric fishing and netting. New Zealand's freshwater fish can be divided into two groups. The first group migrates between freshwater and marine environments at different stages of their lives (diadromous), while the second group remains in freshwater throughout their lives (non-diadromous) (McDowall 1999). In bioegeographic/historical terms, the diadromous species are relatively uninformative, as their much greater dispersal ability enables them to maintain a greater degree of equilibrium in the face of environmental changes than their non-diadromous counterparts. By contrast, the latter appear to show much greater evidence of historic disruption (e.g. Main 1989; McDowall 1996), presumably reflecting their much more limited ability to move between river systems than species that regularly migrate to the sea. They are therefore much more informative about likely geographic patterns in disturbance history, and we rely heavily on their distributional disjunctions in this analysis.

More limited (presence-only) distribution data are available for three groups of invertebrate species; i.e. stoneflies (McLellan 1990), caddisflies (NZ Trichopteran Database: Ward & Henderson 1993) and mayflies (Canterbury Museum: Hitchings 2001). As already indicated, the majority of these data are for species with records of presence (verified by collection), but with no record of absence. Lack of a species record from a particular location may therefore indicate either that the location was searched but the species does not occur there, that no collections have been made there, or that the species occurs there but its occurrence was not of interest at the time. Distribution patterns of some terrestrial species (e.g. plants, land snails) with poor dispersal abilities were also used to corroborate some boundaries, particularly where data for aquatic species were limited.

2.2 GENETIC DATA

Genetic analyses have been carried out for a limited range of New Zealand freshwater vertebrate species. The most comprehensive are those for a closely related group of non-diadromous *Galaxias* species occurring mostly in the southern two-thirds of the South Island (Waters & Wallis 2000, 2001a, 2001b; Waters et al. 2001). A more limited analysis has been carried out for mudfish (*Neochanna* spp.) in the northern North Island (Gleeson et al. 1999; Ling et al. 2001) and in Canterbury (Davey et al. 2003). Ling et al. (2001) examined genetic relationships between riverine and landlocked lacustrine populations of *G. maculatus* and *G. gracilis* in the northern North Island, while Allibone (2002) examined the genetic relationships between *G. divergens* throughout its present range, including North and South Island populations. Unpublished data for *Gobiomprphus breviceps* (P.J. Smith, NIWA, pers. comm. 2003) were used to corroborate some boundaries, and information was also drawn from a recent analysis of genetic differences between widely dispersed populations of the frog *Leiopelma hochstetteri* (Gemmell et al. 2003).

Among freshwater invertebrates, analyses have been made of regional-scale genetic variation in a few species of caddisfly, dobsonfly and/or mayfly, predominantly in the northern North Island (Smith & Collier 2001; Hogg et al. 2002; Smith et al. 2005), for amphipods, mostly at estuarine sites (Schnabel et al. 2000) and for isopods in southern New Zealand (M. Stevens, pers. comm.).

2.3 PHYSICAL DATA

The physiography and geological character of New Zealand was classified into six broad groupings using a digital copy of the 1:1 000 000 map of New Zealand's geology from Suggate (1978). A map showing the accumulated thickness of rhyolitic tephra emanating from the Taupo Volcanic Zone over the last 50 000 years was based on a compilation of published maps of individual tephra from a wide range of sources including published papers and theses (J. Leathwick, unpubl. data). Descriptions of the likely changes occurring during the Last Glacial Maximum were derived from existing published sources (e.g. Porter 1975; Newnham et al. 1989, 1999; Newnham & Lowe 1991; Pillans et al. 1993).

2.4 BOUNDARY DELINEATION

Boundaries were delineated using a subjective, consensus-based approach during a 1-day workshop convened for that purpose and attended by 12 scientists with expertise mostly in the distributions and/or genetics of aquatic biota. Biological data were reviewed initially, with that for non-diadromous fish given the most weight over much of New Zealand, reflecting the availability of data for these species and their relatively limited ability to reoccupy areas from which they have been displaced by physical disturbance (McDowall 1999). Emphasis was placed on defining discrete geographic provinces likely to have experienced similar effects from large-scale disturbances such as glaciation and volcanism at two levels of spatial resolution, referred to below as provinces and units.

Where possible, catchments were used as the fundamental geographic unit from which units and provinces were built up, reflecting the generally greater ease of movement for aquatic species within rather than between catchments. These were aggregated into larger units, taking account of both the potential for inter-catchment dispersal (for example, via drainage networks on common flood plains) and the presence of major geographic barriers to dispersal (such as mountain ranges). The effects of known headwater capture events (through tectonic or glacial activity), and/or historic linkages between catchments (e.g. across coastal plains that were enlarged during periods of lower sea levels) were also considered. Less weight was placed upon terrestrial dispersal pathways, as these tend to favour more vagile species (e.g. winged adults) that exhibit distribution patterns that correspond less closely to catchments (Abell et al. 2000). Offshore islands have been placed into the units with which they shared close connections during the Last Glacial Maximum, when the sea level was approximately 120 m lower than at present (Newnham et al. 1999).

Overall, inferences concerning disturbance effects were based on both physical and biological (species distribution and genetic) data. Some units were distinguished on the basis of the occurrence of particular species or combinations of non-diadromous fish species, while others were distinguished by the widespread absence of non-diadromous species. Information on the distributions of invertebrate species was also taken into account (where available), while genetic differences between populations of individual species were given the least weight, as was distributional information from poorly dispersing terrestrial species. In Northland, where the effects of recent volcanism and climatic change during the Last Glacial Maximum are likely to have been more muted, tentative subdivisions have been based on the potential for dispersal via marine environments.

3. Results

A total of seven provinces and 29 units were defined (Fig. 1). Each of the provinces contains a set of geographically contiguous units, reflecting the importance of similarities in the dominant drivers of broad-scale disturbance, and of geographical linkages likely to facilitate the recovery of species through recolonisation from refugia. Stewart Island/Rakiura forms the most southern unit, while 13 units are defined in the South Island and 15 in the North Island.

3.1 NORTHERN NORTH ISLAND PROVINCE

The Northern North Island Province contains a complex mix of landforms, reflecting the diverse range of underlying geological substrates that include hard older greywacke, softer younger sandstones and mudstones, relatively erosion-resistant volcanic rocks (mostly basalts), and recent (Pleistocene) sediments that form extensive dunes along the west coast and in the north (Ballance & Williams 1982). The four units it contains are typified by relatively muted impacts during the Last Glacial Maximum. Forest is likely to have remained dominant across much of this province through this period (McGlone 1988), resulting in a much more stable landscape than occurred over much of the rest of New Zealand at that time. All of the offshore islands around the northern North Island would have been connected to the mainland in this period, with the exception of The Three Kings islands (Newnham et al. 1999). However, non-diadromous fish are lacking from all of these units, although several support populations of diadromous species. Volcanism has had an intermittent influence during the Pleistocene, with localised basaltic eruptions occurring in northeastern Northland as recently as 1300 years ago, and around Auckland in the last few hundred years (Briggs et al. 1994). A major eruption of rhyolitic tephra affected southern Coromandel around 7000 years ago. The northern North Island is considered a region of high mayfly diversity (Towns 1987; Collier 1993), but has low caddisfly diversity (Henderson 1985).

3.1.1 Northland units

A southern boundary has been drawn to separate the three Northland units from the more disturbance-prone landscapes around Auckland, with their recent eruptions from basaltic cones such as Rangitoto, Mount Eden and One Tree Hill.

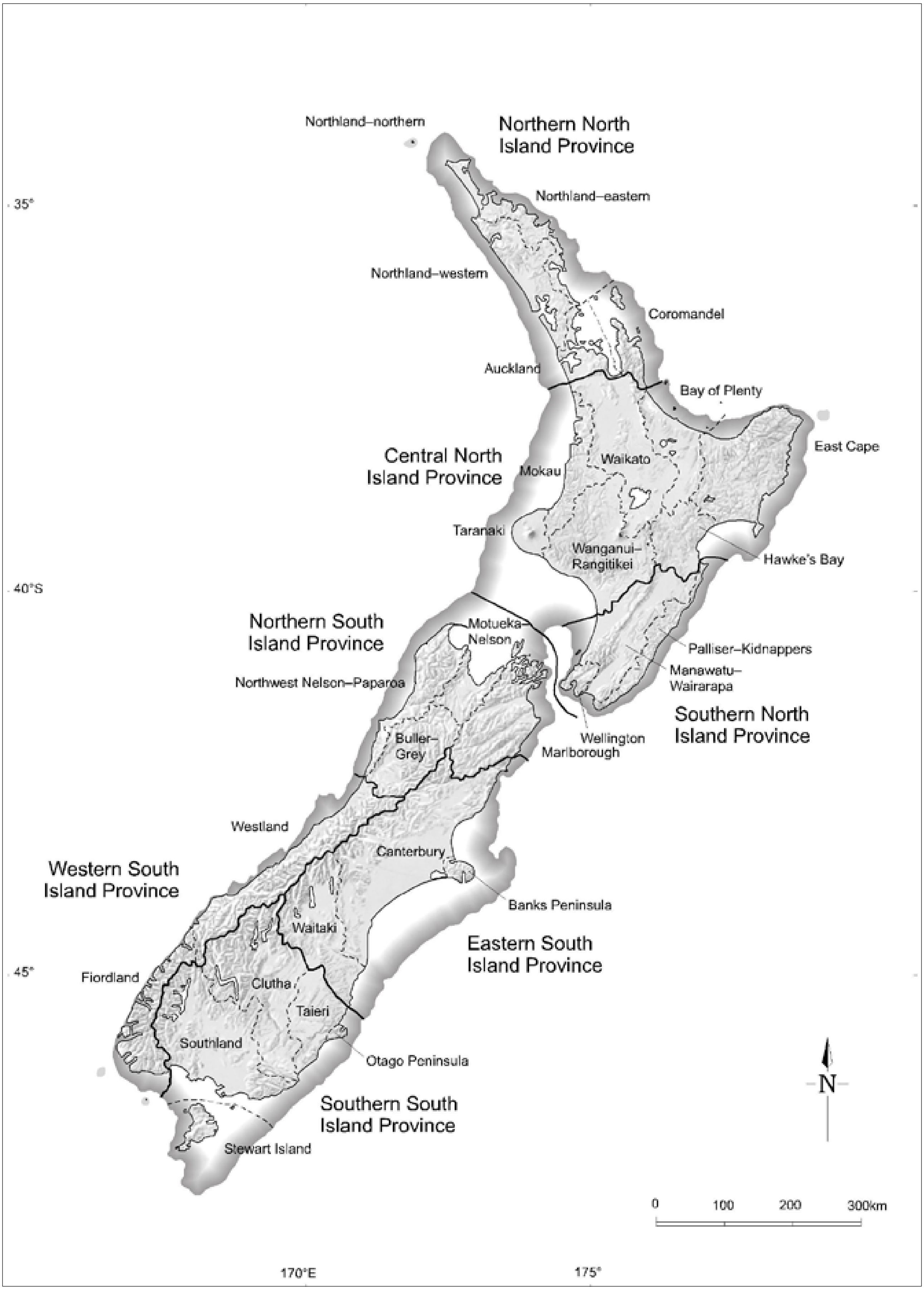

Figure 1. Biogeographic provinces and units relevant to the distribution of freshwater biota. The likely extent of New Zealand at the Last Glacial Maximum is indicated in grey.

The Northland units include all the west-draining catchments flowing into the Kaipara Harbour, the small catchments and lakes of the dunelands along the west coast south of the Kaipara Harbour to just north of the Hunua Ranges, and the east-draining catchments north of Cape Rodney. Offshore there are the Cavalli Islands, Poor Knights Islands, Hen and Chickens Islands and Mokohinau Islands, with many of the smaller islands of these groups lacking permanent fresh water.

Subsequent subdivision of Northland separates east- and west-draining streams and rivers of hill country through the bulk of Northland, reflecting their different linkages via marine connections, and the likely difficulties in dispersal between the east and west coasts caused by the strong tidal streams around North Cape. Biological evidence in support of this distinction is provided by the non-diadromous fish *Gobiomorphus basalis* and three species of freshwater snail, all of which are much more widespread in west-draining catchments than in the east (M. Haase, NIWA, pers. comm. 2003). These distribution patterns may also reflect the larger extent of some of the west-draining catchments (e.g. the Wairoa) compared with those draining to the east. The second subdivision separates the sand dune-dominated topography of the far north from the Northland 'mainland', with evidence for a lack of contemporary genetic connection across this boundary being found in *Neochanna diversus* by Ling et al. (2001).

Distinctive biological features of the Northland units include their high diversity of mayflies (Towns 1987; Collier 1995), while McLellan (1990) describes marked differences in stonefly assemblages between Auckland and Northland. By contrast, Northland has low caddisfly diversity (Henderson 1985). Two regionally endemic species of non-diadromous fish occur in Northland—*Galaxias gracilis* and *Neochanna heleios*. Other non-diadromous fish occurring in Northland are *Gobiomorphus basalis* and *Neochanna diversus*. Studies of the genetic structure of several stream invertebrates have identified, for three species, marked inter-population differences between individuals collected in Northland and those collected further south, including around Auckland and/or in the Waikato (Smith & Collier 2001; Hogg et al. 2002; P.J. Smith, NIWA, pers. comm. 2003).

A recent analysis of genetic structure in different populations of *Leiopelma hochstetteri* also identifies a distinctive Northland clade (Gemmell et al. 2003).

3.1.2 Auckland unit

This unit is the area south of a line running from Cape Rodney in the east to the northern side of the Waitakere Ranges, and north of a line extending eastwards from Port Waikato along the northern boundary of the Waikato catchment to include the Hunua Range and small catchments draining into the western shores of the Firth of Thames. The unit includes numerous offshore islands including Kawau, Tiritiri Matangi, Rangitoto, Motutapu, Waiheke and Ponui. As already indicated, a more dynamic history is likely for this unit, with periodic eruptions of basaltic volcanoes around Auckland City, the most recent occurring only c. 500 years ago (Briggs et al. 1994). In addition, the narrow neck of low-lying land between the Manukau and Waitemata Harbours has at times been under water, and is likely to have provided a significant barrier to the dispersal of some organisms. Activity in the nearby South Auckland volcanic field occurred much earlier than around Auckland City, largely ceasing about 500 000 years ago (Briggs et al. 1994), while the andesitic eruptions that formed the Waitakere Ranges were much older, occurring during the Miocene. *Gobiomorphus basalis* is the only non-diadromous fish species occurring in this unit, but it is widespread, except in the southeast.

3.1.3 Coromandel unit

This unit is centred on the Coromandel Peninsula, extending south to include the Kauaeranga catchment near Thames in the west, and to the northern end of Waihi Beach in the east. Several islands are included in this unit, i.e. the small islands of the eastern Hauraki Gulf, Great Barrier Island (Aotea Island), Hauturu/Little Barrier Island, Cuvier Island (Repanga Island), Mercury Islands, The Alderman Islands, and Slipper Island (Whakahau). Larger islands such as Great Barrier Island (Aotea Island), Hauturu/Little Barrier and Great Mercury Island (Ahuahu) have significant freshwater streams, some of which contain diadromous fish species (NZ Freshwater Fish Database, NIWA). As with Northland, much of this unit probably remained forested during the Last Glacial Maximum except at higher elevations (McGlone 1988), and therefore has a relatively stable recent past. Much of the unit is composed of andesitic rocks dating from the Miocene, while rhyolitic volcanic eruptions are likely to have had at least some impact, mostly in the southeast, with the most recent major tephra emanating from Mayor Island (Tuhua) a little over 6000 years ago (Newnham et al. 1999). Catchments are typically small and steep through much of the unit, with only a few larger rivers having well-developed flood plains in their lower reaches. *Gobiomorphus basalis* is the only non-diadromous fish species present. Terrestrial evidence corroborating the distinctive character of this unit includes the occurrence of three endemic plants and at least two large endemic invertebrates restricted to Moehau (A. Roxburgh, pers. comm.), and the distinctive genetic character of North Coromandel/Great Barrier Island populations of the frog *Leiopelma hochstetteri* (Gemmell et al. 2003).

3.2 CENTRAL NORTH ISLAND PROVINCE

Volcanism is the dominant feature of the central North Island, with its province containing the andesitic volcanoes of Taranaki and the Tongariro Volcanic Centre, and the rhyolitic volcanic centres (e.g. Taupo, Maroa, Okataina) of the Taupo Volcanic Zone. Surrounding this zone are extensive areas of mountains and hill country, including uplifted Mesozoic greywacke ranges such as the Ruahine Range, Kaimanawa Mountains, and Ahimanawa, Urewera and Raukumara Ranges to the east, and the Hauhungaroa Range to the west. Dissected, lower-elevation hill country at greater distances from the Taupo Volcanic Zone is generally formed from younger and softer Tertiary sedimentary rocks, i.e. sandstone, siltstone and mudstone. Eruptions emanating from the Taupo Volcanic Zone, and affecting the surrounding hill country, have generally consisted of both high-energy, incandescent, gas-charged clouds of flow material (ignimbrite) and cooler air-fall deposits (tephra), the latter generally extending further from the eruption source than the former (Walker 1980). A total of 36 tephras have been identified from the last 50 000 years of activity (Froggatt & Lowe 1990), the largest of these, which occurred approximately 23 000 years ago, producing at least 220 km^3 of material. While this eruption would have affected most of the central and lower North Island and the northeast of the South Island, many other eruptions have produced more localised effects. The zone of greatest cumulative impact is centred northeast of Rotorua, with the total depth of erupted material approaching 50 m. The southern boundary of this province broadly coincides with the major change in caddisfly assemblages observed by Henderson (1985) and the southern limits of several mayfly species (e.g. *Austronella planulata*) (Hitchings 2001).

3.2.1 Waikato unit

The Waikato unit consists of the Waikato, Waihou and Piako catchments, and includes hydro dams located along the middle reaches of the Waikato River, and a number of natural riverine lakes, mostly of limited extent, scattered across the extensive alluvium deposited by the Waikato River in its lower reaches. Although all three larger river systems have been subject to major impacts from rhyolitic eruptions, all have some lower tributaries (e.g. the Waipa flowing into the Waikato) that are either distant from eruption sources, and/or have been minimally affected by water-transported eruption debris, and are therefore likely to have provided refugia during periods of otherwise widespread devastation (McDowall 1995, 1996). *Neochanna diversus* is widespread in the wetlands and small streams draining the extensive Quaternary surfaces of the lower Waikato and Piako, and *Gobiomorphus basalis* is common in hill-country streams and rivers of the lower reaches of the catchment. Other non-diadromous species are generally rare in the lower Waikato, with only one record for *Galaxias divergens* in the Waihou River. No non-diadromous fish are known from the upper Waikato catchment, where the effects of rhyolitic ignimbrite eruptions were most severe, and where major waterfalls or rapids provide significant barriers to fish passage. Landlocked populations of normally diadromous species in Lake Taupo, such as *Retropinna retropinna*, were possibly introduced as a food source by Maori (McDowall 1996). Populations of the caddisfly *Orthopsyche fimbriata* collected within the Waikato unit were genetically distinct from those in Northland (Smith & Collier 2001), and more recent evidence for the mayfly *Acanthophlebia cruentata* suggests a similar pattern, with Waikato populations distinct from those in Auckland (Waitakere Ranges), Bay of Plenty and Mokau (Smith et al. 2005).

3.2.2 Mokau unit

Small, steep coastal catchments are the dominant feature of the Mokau unit, all draining into the Tasman Sea along the North Island's west coast from just south of Port Waikato to northern Taranaki. Geologically, it consists of a mix of sandstone, mudstone and limestone, some older sedimentary rocks, and some volcanic rocks. The largest rivers are the Marokopa, Awakino and Mokau. A number of dune lakes occur along the coast, the largest of which is Lake Taharoa. All parts of the Mokau unit would have been affected to some degree by the voluminous Kawakawa tephra erupted around 23 000 years ago from the Taupo Volcanic Centre. However, the unit would have been much less affected by subsequent eruptions from Taupo than the Waikato River and catchments in the Bay of Plenty and central Hawke's Bay. As in Coromandel, many catchments are small and steep with few large flood plains. Non-diadromous fish are rare; *Gobiomorphus basalis* occurs at a few sites in the north, *G. breviceps* occurs in the Mokau River and *Neochanna diversus* is recorded at its southern limit from one site in the northern headwaters of the Mokau River, close to the boundary with the Waikato catchment. However the restricted distribution of the latter may simply reflect a relative lack of suitable wetland habitat.

3.2.3 Bay of Plenty unit

This unit encompasses catchments flowing into the Bay of Plenty from the northern part of the Taupo Volcanic Zone, the largest catchments being the Kaituna and Rangitaiki. It also includes a number of lakes, the larger of which mostly occur in collapsed calderas left after large rhyolitic eruptions, while smaller lakes generally occupy old explosion craters (Lowe & Green 1987). The larger catchments, in particular, have been exposed to severe disruption from older eruptions of ignimbrite and from air-fall deposition of tephra, resulting in the development of a coastal plain built up predominantly from water-transported rhyolitic material, large areas of which are overlain with accumulations of peat. The majority of this unit would have been affected by deposition of Kaharoa Ash, a sandy tephra erupted approximately 770 years ago from Mt Tarawera (Froggatt & Lowe 1990). The non-diadromous fish fauna consists of isolated populations of *Gobiomorphus basalis* and *Galaxias divergens*, the first mostly in coastal sites and the latter in one or two lower tributaries of the Rangitaiki River. Offshore islands include Mayor Island (Tuhua), Motiti, Moutohora and Whakaari/White Island. Mayor Island (Tuhua) supports a number of freshwater lakes and small streams but we are unaware of any fish distribution records from these.

3.2.4 East Cape unit

Rivers and streams in this unit, which extends from the Whakatane River in the Bay of Plenty, around East Cape and south to the Waihua River in Hawke's Bay, typically drain steep, dissected hill country formed from Mesozoic greywacke, sandstone and siltstone (west), or younger Tertiary siltstone, sandstone and mudstone (east). Major catchments include the Whakatane, Waimana, Waioeka, Motu, Raukokere, Mata, Waipaoa and Wairoa Rivers. It also includes a number of lakes, most of which (including Lake Waikaremoana), are formed by landslides that have blocked water courses (Lowe & Green 1987). The unit has suffered periodic disruption by air-fall tephra ejected during rhyolitic eruptions from the Taupo Volcanic Zone, with the cumulative depth of tephra deposited over the last 50 000 years decreasing from approximately 10 m in the headwaters of the Whakatane River to less than 50 cm towards East Cape. The relatively impoverished nature of the non-diadromous fish fauna is most likely a direct consequence of this recurrent disturbance (McDowall 1995, 1996), with *Gobiomorphus basalis* the only species present. Populations of the frog *Leiopelma hochstetteri* in the East Cape region show distinct genetic differences from populations elsewhere in the upper North Island (Gemmell et al. 2003).

3.2.5 Taranaki unit

This unit comprises the streams and small rivers that drain the andesitic strato-volcanoes of Taranaki, Pouakai and Kaitake and their surrounding ring-plain. Two sub-catchment categories are included in this unit: one for sub-catchments draining the volcanic ring plain and the second for those draining the dissected hill country to the east. More specifically, the western headwaters of the Patea River, which descend the eastern flanks of Taranaki, are separated from the remainder of the Patea River just below Stratford, while the Manganui (a tributary of the Waitara River) is included from its headwaters to the sea, while the main west-flowing stem of the Waitara River is placed in the Mokau unit. Volcanism provides the dominant physical disturbance in this unit, with at least 76 major distinct tephra eruptions having occurred over the last 28 000 years

(Alloway et al. 1995). Three non-diadromous fish species occur in this unit, with *Gobiomorphus basalis* and *G. breviceps* the more widespread, although both occur only in catchments draining the eastern side of Mt Taranaki. *Neochanna apoda* is recorded at a few lowland sites, but its restricted range may simply reflect the relative scarcity of suitable habitat in this unit. Taranaki populations of the mayfly *Acanthophlebia cruentata* show DNA haplotypes distinct from those found in Waikato populations (Smith et al. 2005).

3.2.6 Wanganui–Rangitikei unit

The Wanganui–Rangitikei Unit encompasses rivers and streams draining into the South Wanganui Bight from the eastern margins of the Taranaki ring-plain southeast to the Rangitikei River. Larger rivers such as the Rangitikei, Wanganui, Waitotara and Patea arise in the hill country around the western and southern margins of the volcanic plateau, and are likely to have been periodically devastated by rhyolitic eruptions from the Taupo Volcanic Centre, with terraces formed from debris from the Taupo Pumice eruption still evident; for example, along the Wanganui River (Suggate 1982). In addition, these rivers would also have been periodically affected by cold air-fall andesitic ash from eruptions of the Tongariro and Taranaki Volcanoes, and acidic water and debris from lahars has affected those rivers arising from Ruapehu, particularly the Wangaehu. As many of these rivers are deeply incised into younger Tertiary and Lower Quaternary sedimentary rocks, their lower reaches and/or tributaries probably provided refugia for at least some freshwater biota during these disruptions. A number of small lakes occur towards the coast, either in dunelands or in hill country where landslides have blocked water courses. *Gobiomorphus basalis* and *G. breviceps* are the only widespread non-diadromous fish present. *Neochanna apoda* occurs in the lower Rangitikei and *Galaxias divergens* is recorded from the upper reaches of catchments draining the western side of the Ruahine Range.

3.2.7 Hawke's Bay unit

The Mohaka and Ngaruroro Rivers, both of which received moderate to deep deposits of rhyolitic flow material in their headwater streams (e.g. Wai-tu-pirita, Oamaru, Waipunga) during the Taupo eruption of around AD 181, dominate this unit. Air-fall tephra would also have been deposited over the majority of the unit during this and other eruptions from the Taupo Volcanic Zone (McDowall 1995), and the steep terrain is likely to have contributed to prolonged inputs of ash into rivers from ongoing erosion. The unit also includes Lake Tutira, which was formed by a large landslide. Non-diadromous fish species occur only infrequently, with three species present: *Galaxias divergens*, *Gobiomorphus breviceps* and *G. basalis*.

3.3 SOUTHERN NORTH ISLAND PROVINCE

The Southern North Island Province is dominated by large river systems that drain the main axial ranges (Ruahines and Tararuas) and/or the lower-elevation hill country that extends from Cape Kidnappers to Cape Palliser. It also includes the extensive alluvial plains and/or sediment-filled depressions of Manawatu, southern Hawke's Bay and Wairarapa. In late Tertiary times, this region experienced severe disruption by marine transgression, with many of the younger sedimentary rocks dating from this period. However, the Tararua and Ruahine Ranges, which are formed by orogenic uplift of older Mesozoic greywacke rocks, may have protruded above sea level at this time (Heerdegen 1982), as would have some of the uplifted ranges to the east (Kamp 1982). At a regional scale, volcanism has had much less impact than further north in the central North Island, although major events such as the Kawakawa eruption of 23 000 years ago would have had at least some impact, initiating a major period of landscape instability during the Last Glacial Maximum (Pillans et al. 1993). The province also experienced considerable depression of snow lines during this period, particularly around Cook Strait, but only limited glacial sculpturing occurred on the Tararua Range (Stevens 1974). At this time, the coastal plain along the Manawatu Coast extended across the northern entrance of Cook Strait to provide a connection with the northern South Island, with the Strait reduced to a deeply incised bay. Enlargement of the coastal plain would have been much less dramatic along the Wairarapa and Hawke's Bay coast. Relatively recent tectonic movement has profoundly affected some catchments around Wellington.

3.3.1 Manawatu–Wairarapa unit

This extensive unit is dominated by large river systems that have at least some tributaries that arise in steep upper catchments formed from uplifted Mesozoic greywacke, with many tributaries flowing across extensive lowland alluvial plains. The largest catchments are the Tukituki, which drains into Hawke's Bay, the Manawatu, Ohau, Otaki and Waikanae Rivers which drain into the Tasman Sea, and the Ruamahanga River and its tributaries that flow into Palliser Bay. Unstable dune country occurs along the Manawatu coast where small dune lakes are relatively common, and several riverine lakes occur in the Hawke's Bay lowlands, and Lake Wairarapa and a number of shallow lagoons occur in the lower reaches of the Ruamahanga River. Kapiti Island, lying off the southern part of the west coast, is included in this unit. The non-diadromous fish fauna is one of the more diverse in the North Island, consisting of *Galaxias divergens*, *Gobiomorphus breviceps*, *G. basalis* and *Neochanna apoda*.

Past linkages between the Tukituki, Manawatu and Ruamahanga Rivers are reflected in the genetic similarities of their current populations of *Galaxias divergens* (Allibone 2002) and *Gobiomorphus breviceps* (P.J. Smith, NIWA, pers. comm. 2003). In addition, genetic similarities of populations of *Galaxias divergens* and of *Gobiomorphus breviceps* in the Manawatu and the Marlborough Sounds probably result from interchange of genetic material which occurred during the Last Glacial Maximum, when these two provinces were connected as a consequence of the closure of Cook Strait by lowered sea levels.

3.3.2 Palliser–Kidnappers unit

This elongated unit consists of numerous, mostly small, catchments draining steep hill country formed from Mesozoic to Oligocene sedimentary rocks along the east coast of the southern North Island. While these catchments have been much less affected by volcanism than have those further north, their small size, combined with their relative lack of coastal plains, even during the Last Glacial Maximum, is likely to have resulted in a relatively high vulnerability to extinction. Recolonisation by less mobile species is probably hindered by the relatively well-defined ranges separating this unit from the adjacent Manawatu–Wairarapa Unit. The non-diadromous fish fauna consists of only one species, *Gobiomorphus basalis*.

3.3.3 Wellington unit

This unit comprises the hill country of Wellington and the southern parts of the Tararua and Rimutaka Ranges, the largest catchments being the Hutt, Wainuiomata and Orongorongo Rivers. Mana and Matiu/Somes Islands are also included in this unit. Some river systems in this unit have been subject to major disruption by fault movement. For example, the rivers and streams that once formed the Pauatahanui Estuary are now greatly diminished in size as a consequence of development of the Wellington Fault (Stevens 1974). *Gobiomorphus basalis*, *G. breviceps* and *Galaxias divergens* are the only non-diadromous fish recorded, all three occurring only sporadically, with the last having genetically distinct populations from those further north (Allibone 2002). Also, Wellington populations of *Gobiomorphus breviceps* are genetically distinct from populations in the Manawatu–Wairarapa unit (P.J. Smith, NIWA, pers. comm. 2003). Henderson (1985) identified the Rimutaka and southern Tararua Ranges as a centre of caddisfly diversity.

3.4 NORTHERN SOUTH ISLAND PROVINCE

While glaciation rather than volcanism probably provides the major contemporary driver of biogeographic pattern in the South Island, studies of the physical effects of the Last Glacial Maximum suggest marked spatial variation in its impacts (Newnham et al. 1999). For example, ice cover is presumed to have been most extensive on the higher elevation parts of the Southern Alps/Ka Tiritiri o te Moana (i.e. occurring almost continuously from Nelson Lakes in the north to southern Fiordland) with snow lines depressed by 600–800 m. In the west, ice descended to form piedmont glaciers that covered much of the coastal plain in Westland (Soons 1982); while to the east, glaciers carved out the major lakes that include Lakes Sumner, Coleridge, Tekapo, Pukaki, Ohau, Hawea, Wanaka and Wakatipu. The Northern South Island Province was probably less affected by these events than regions further south, with extensive areas of lower-elevation hill country and/or alluvium whose catchments could potentially provide refugia for non-diadromous fish and other fauna. However, the extensive deposits of glacial gravels in rivers such as the Motueka and Wairau indicate that glaciation has had at least some effect.

Less is known about the relationships between fish distributions and the large-magnitude earthquakes that occur at intervals in this province (Suggate 1982). These have considerable potential to initiate major landscape instability, with the *M* 7.7 Murchison earthquake initiating landslides that produced an average debris yield of 210 000 m^3/km^2 across a 1200 km^2 survey area (Pearce & O'Loughlin 1985). Some of the landslides initiated by these large-magnitude earthquakes also formed lakes by damming water courses, some of these persisting for lengthy periods until in-filled by alluvial material (Adams 1981). Evidence from Lake Matiri, north of Murchison, suggests that considerable disruption may also occur in water courses below such impoundments as a result of mudflows formed when landslides are overtopped by backed-up water.

The northwest Nelson region is known as an area of stonefly and caddisfly endemicity (Henderson 1985; McLellan 1990) and it marks the southern limit of several mayfly species widespread throughout the North Island (e.g. *Zephlebia dentata*, *Z. versicolor*) (Hitchings 2001).

3.4.1 Northwest Nelson–Paparoa unit

This unit comprises extensive areas of steep mountainous country formed from rocks of widely varying ages, including extensive older (Palaeozoic to Mesozoic) granite, greywacke, limestone and marble, and younger (Miocene to Eocene) sandstone, siltstone and limestone. As indicated above, this unit was probably much less affected by glaciation during the Last Glacial Maximum than units located further south, particularly those along the Southern Alps. It includes major river systems such as the Mokihinui, Karamea, Heaphy, Aorere and Takaka Rivers. It contains a very low diversity of non-diadromous fish, with only one widespread species, *Gobiomorphus breviceps*, recorded predominantly from coastal or lowland streams. *Neochanna apoda* occurs in several wetlands throughout the unit. Although links between this impoverished fauna and the effects of periodic large magnitude earthquakes can only be speculated about, a study of forest dynamics in this unit confirms the sensitivity of these catchments to large-scale, earthquake-triggered disturbances (Vittoz et al. 2001). A collation of collection records for stoneflies (McLellan 1990) identifies this as one of two South Island regions having high species richness within this group, and a number of locally distributed caddisflies occur in northwest Nelson (Collier 1993), and four endemic genera of aquatic snails occur only in this unit (M. Haase, NIWA, pers. comm. 2003).

3.4.2 Motueka–Nelson unit

This unit consists of several catchments, the largest being the Motueka and Waimea Rivers, which flow into Tasman Bay between Separation Point in the west and Cape Soucis (Raetihi) (just south of Croisilles Harbour) in the east. The extensive areas of dissected glacial outwash (Moutere) gravels provide clear evidence of the historic impacts of glaciation in this unit, although parts of both major catchments as well as many small catchments drain hill country formed mostly from sedimentary or metamorphic rocks. *Galaxias divergens* (western) and *Gobiomorphus breviceps* are the only widespread non-diadromous fish species present, while *Galaxias vulgaris* has been recorded from one site in the headwaters of the Motueka River. Populations of *G. divergens* in the Motueka catchment are genetically distinct from those found in neighbouring Buller–Grey and Marlborough Units (Allibone 2002), and a similar difference occurs between the respective populations of *Gobiomorphus breviceps* in these units (P.J. Smith, NIWA, pers. comm. 2003).

3.4.3 Marlborough unit

This topographically diverse unit encompasses the Marlborough Sounds, the Richmond Ranges, and the major catchments of central and southern Marlborough, i.e. the Waiau, Awatere and Clarence Rivers. Also included are several islands in the Marlborough Sounds, the larger of which (i.e. Arapawa and Rangitoto ke te Tonga (D'Urville Island)) have significant freshwater streams. The unit contains a number of coastal barrier lakes, of which the largest is Lake Grassmere/Kapara Te Hau, with smaller lakes occurring on D'Urville Island. The non-diadromous fish fauna is dominated by *Galaxias vulgaris*, *G. divergens* and *Gobiomorphus breviceps*, with a few records for *Galaxias paucispondylus*. Studies of genetic similarities in *G. vulgaris* (Waters & Wallis 2001b) indicate that populations of this species in the Clarence River are more closely related to those in the Wairau headwaters than to populations further south in Canterbury, with the low passes between the Clarence and Wairau River headwaters to the north presumably increasing the chances of headwater stream capture events that would facilitate interchange between these populations. However, low passes also occur between the Clarence and Waiau Rivers to the south. Fish specimens referred to as *Gobiomorphus alpinus* have been collected from tarns or small lakes in the headwaters of the Clarence and Wairau Rivers, but the status of this species is not resolved with certainty (Smith et al. 2003). Populations of *G. breviceps* from the Branch River are genetically differentiated from populations in the Motueka–Nelson and Grey–Buller units (P.J. Smith, NIWA, pers. comm. 2003). Marlborough represents the southern limit of *Paranephrops planifrons* on the east coast of the South Island.

3.4.4 Grey–Buller unit

This unit encompasses the two most geographically extensive river systems of the South Island's West Coast, these flowing from glacial-sculpted, sometimes lake-fed headwaters, through extensive lowland deposits of glacial till and alluvium. Six non-diadromous fish species occur in this province, contrasting with rivers further south in Westland and Fiordland (Main 1989), and presumably reflecting the lesser impacts of glaciation, perhaps combined with the presence of more extensive lowland streams and rivers capable of providing refugia during glacial maxima. *Galaxias divergens* and *Gobiomorphus breviceps* are widespread, but *Galaxias vulgaris*, *G. prognathus* and *G. paucispondylus* occur at only a few sites in the east in the headwaters and upper reaches of the Maruia River. Although the isolated outlier of *G. vulgaris* has been interpreted as indicating historic linkages with Marlborough populations of this species, probably in the vicinity of Nelson Lakes (Waters & Wallis 2000), Soons (1982) argues for historical connection of the Maruia headwaters with the upper Lewis, a tributary of the Waiau River. *Neochanna apoda* has been reported from one site near Greymouth.

3.5 WESTERN SOUTH ISLAND PROVINCE

The Western South Island Province encompasses those parts of the South Island likely to have been most severely affected by glaciation during the Last Glacial Maximum (see above), with the widespread disruption of freshwater systems presumed to have largely eliminated non-diadromous fish species. Although seismic activity has probably been less frequent in Westland than further north, major earthquakes occur relatively frequently in Fiordland (Suggate 1982).

3.5.1 Westland unit

The Westland unit extends along the South Island's west coast from the Taramakau River in the north to the Hollyford River/Whakatipu Ka Tuka in the south, encompassing such major river systems as the Hokitika, Whataroa, Karangarua, Paringa, Haast and Arawhata. This unit also includes a number of lowland lakes, most of which are of glacial origin. The general paucity of non-diadromous fish in this unit most likely reflects the impacts of glaciation (Main 1989), with piedmont glaciers extending along much of the coastal plain during the Last Glacial Maximum (Soons 1982). However, post-glacial dispersal has clearly also been hindered by the high elevation of the Southern Alps. The only non-diadromous fish occurring in the unit are *Galaxias divergens* and *Gobiomorphus breviceps*, which both occur south to the Hokitika River, and *Neochanna apoda*, which occurs in lowland sites as far south as Okarito (presumably reflecting a slow southern recolonisation from the less disturbed Grey–Buller unit to the north). This unit also represents the southern limit on the west coast for *Paranephrops planifrons*, which is widespread in the North Island and the west and north of the South Island. A range of diadromous *Galaxias* species is widespread.

3.5.2 Fiordland unit

This unit, which extends from just north of Milford Sound/Piopiotahi south to Long Sound, includes numerous rivers and large numbers of glacially-carved lakes that range in size from small tarns to extensive lakes, the latter mostly in the south. It is notable for its complete absence of non-diadromous fish, presumably reflecting the influence of glaciation and the lack of lowland refugia close inshore (Main 1989), and perhaps the effects of relatively frequent seismic activity. Marine currents flowing south along the western Fiordland coast and then east around the South Island's south coast (Carter et al. 1998) are likely to present a considerable barrier to westward coastal migration of non-diadromous fish species from Southland. This unit coincides with one of two South Island regions reported as having a high richness of stoneflies (McLellan 1990), and also supports a number of caddisflies of restricted geographic range. Numerous islands are included in this unit, the largest of which are Secretary and Resolution Islands. *Paranephrops zealandicus* replaces *P. planifrons* as the freshwater crayfish species in this unit. Genetic analysis of the freshwater isopod, *Austridotea lacustris*, a widespread species in the southern South Island, Stewart Island/Rakiura, Chatham Islands and Campbell Island/Motu Ihupuku (Chadderton et al. 2003), indicates that the Fiordland populations are distinct.

3.6 EASTERN SOUTH ISLAND PROVINCE

The Eastern South Island Province extends from the Hapuku and Kahutara Rivers that drain the southeastern slopes of the Seaward Kaikoura Range, south to the Waianakarua and Kakanui Rivers that drain the northern side of the Kakanui Mountains. While this province lacked the extensive piedmont ice cover that developed at similar elevations in Westland, glaciers in the upper reaches of major east-flowing rivers were large enough to produce copious amounts of debris, which washed downstream to be deposited on the Canterbury Plains. A series of high-country lakes including Lakes Sumner, Coleridge and Heron were also formed by this glacial activity, while Lake Ellesmere (Te Waihora) and Lake Forsyth (Waiwera) are coastal barrier lakes lying inland of the Kaitorete Spit. As a consequence of the lowered sea level, these extended on their seaward side by up to 50–60 km more than at present. In addition, large amounts of finer sediments exposed on the former sea floor by the lowered sea level, or deposited by meandering, debris-choked rivers, were mobilised and blown back inland, forming extensive deposits of loess. The southern boundary of this province broadly coincides with changes in the composition of stonefly fauna (McLellan 1990) and a shift in endemism of caddisfly fauna (Henderson 1985), with several caddis species found only approximately south of this boundary (e.g. *Neurochorema pilosum* and *Psilochorema acheir*).

3.6.1 Canterbury unit

This unit encompasses a large part of the eastern South Island, including the catchments of the Conway, Waiau, Hurunui, Waimakariri, Rakaia and Rangitata Rivers. The Waihao River, a small catchment located just north of the Waitaki River mouth, forms the southern boundary. Most of the larger rivers in this unit have their headwaters in montane catchments spread along the eastern flanks of the Southern Alps, and flow across extensive glacial outwash plains before reaching the Pacific Ocean. The smaller rivers tend to drain the foothills, or are spring-fed. Non-diadromous fish recorded from the province are *Galaxias paucispondylus* (middle and upper reaches of larger rivers), *G. prognathus* (larger river headwaters, mostly from the Rakaia and south), *Neochanna burrowsius* (lowlands) and *G. vulgaris* and *Gobiomorphus breviceps* (both widespread). Evidence from two studies suggests a high degree of genetic homogeneity in freshwater fish within this province, both *Galaxias vulgaris* (Waters & Wallis 2001b) and *N. burrowsius* (Davey et al. 2003) showing little differentiation across a range of Canterbury sites. Stokell's smelt (*Stokellia anisodon*), a diadromous species of restricted geographic range, occurs only in the lower reaches of several of the major rivers of this unit.

3.6.2 Banks Peninsula unit

This unit contrasts sharply with the preceding unit, consisting of small, steep catchments flowing off the old (Miocene to Pliocene) weathered basaltic cones that form Banks Peninsula. Extensive deposits of loess cover much of the peninsula, suggesting minimal vegetation cover during at least parts of the Last Glacial Maximum. *Gobiomorphus breviceps* is the only non-diadromous fish species present. Several endemic invertebrates occur in streams and rivers in this unit (Harding 2003).

3.6.3 Waitaki unit

This unit includes the main Waitaki catchment, plus smaller coastal rivers draining into the Pacific Ocean to the south as far as Shag Point/Matakaea. Several large glacial lakes occur in the McKenzie Basin, while hydro dams are located in the middle reaches of the Waitaki River. Although the Waitaki headwaters were severely impacted by glaciation, the main river catchment is much more constricted in its lower reaches and therefore probably lacked the meandering connections likely to have occurred further north in Canterbury. However, these connections may have occurred more frequently during the Last Glacial Maximum, when the coastal plain was much more extensive than at present. The unit supports a number of non-diadromous fish species including *Galaxias cobitinis* (scattered and infrequent), *G. paucispondylus* (upper reaches), *G. prognathus* and *G. macronasus* (headwaters), *G. vulgaris* (widespread), and *Gobiomorphus breviceps* (widespread). *Neochanna burrowsius* occurs at a few lowland sites near the boundary with the Canterbury unit described above. *Galaxias macronasus* and *G. cobitinis* occur only in this unit (McDowall & Waters 2002, 2003).

3.7 SOUTHERN SOUTH ISLAND PROVINCE

The Southern South Island Province encompasses one of the more topographically and environmentally diverse parts of New Zealand, including high-elevation mountains of the Southern Alps, lower-elevation ranges and mountains further east, extensive inter-montane basins, rolling down-lands and plains of glacial and/or alluvial origin. While the high-elevation western mountains were undoubtedly affected profoundly by glaciation during the Last Glacial Maximum, lower-elevation units to the east had minimal ice cover, and these less-affected landscapes presumably provided refugia for the diverse non-diadromous fish fauna that survives there now. In addition, land exposed by the sea level lowering connected Stewart Island/Rakiura to the mainland South Island.

3.7.1 Clutha unit

The Clutha unit comprises a single large catchment arising on the eastern slopes of the Southern Alps and flowing through large, glacial-sculpted lakes, while lower tributaries drain the extensive inter-montane basins of central Otago, and the lower-elevation ranges of eastern Otago and Southland. Non-diadromous fish species include *Galaxias anomalus*, *G. pullus*, *Galaxias* sp. D, and *Gobiomorphus breviceps*, all occurring mostly in the lower half of the catchments. A localised population of *Galaxias gollumoides* occurs in the headwaters of the Nevis River, which Waters et al. (2001) interpret as reflecting an ancient drainage connection between this stream and the headwaters of the Mataura River, one of the major catchments of the Southland unit. Similarly, *G. paucispondylus* has been found recently in the headwaters of the Manuherikia River and an isolated population also occurs in the Lochy River, which flows into Lake Wakatipu. The lack of records for the latter two species from elsewhere in the Clutha unit remains a puzzle.

3.7.2 Taieri unit

This unit encompasses rivers and streams flowing into the Pacific Ocean from the Shag River south to the Tokomariro River. The Taieri River is the largest of these, and drains the extensive block mountains and inter-montane basins of eastern Otago. The unit supports a diverse and distinctive collection of non-diadromous fish (Waters & Wallis 2001b), i.e. *Galaxias anomalus* (headwaters), *G. depressiceps* (widespread), *G. eldoni* (lower reaches), *G. pullus* (west) and *Gobiomorphus breviceps* (widespread, and distinct from populations in Southland and Waitaki) (P.J. Smith, NIWA, pers. comm. 2003).

3.7.3 Otago Peninsula unit

This unit provides a similar contrast to the adjacent Taieri Unit as does Banks Peninsula and its neighbour, Canterbury. It consists of numerous small, steep catchments draining dissected, loess-mantled basaltic rocks dating from the upper Miocene. *Gobiomorphus breviceps* is the only non-diadromous fish species reported from this unit. At least two aquatic invertebrate species are endemic to the peninsula (the caddisfly *Pseudoeconesus paludis*, and the isopod *Austridotea benhami*) (Chadderton et al. 2003).

3.7.4 Southland unit

This extensive, predominantly lowland unit includes the Catlins, Tahakopa, Mataura, Oreti, Aparima and Waiau Rivers. The first two of these drain low, dissected hill country cut into the sandstone rocks of the Catlins, while the remaining four rivers have their headwaters further north in the ranges of inland Southland, several of which are lake fed, and which flow across extensive areas of glacial gravels, loess and alluvium in their lower catchments. Some dune lakes occur along the Southland coast. During the Last Glacial Maximum, all the larger Southland rivers would have flowed across a coastal plain extending to Stewart Island/Rakiura and beyond (see Newnham et al. 1999), and genetic evidence confirms historic interchange of individuals between populations in the Oreti, Mataura and Waiau Rivers (Waters et al. 2001). Non-diadromous fish species present in this unit include *Galaxias* 'southern', *Galaxias gollumoides*, *Galaxias* sp. D and *Gobiomorphus breviceps*. *Galaxias paucispondylus* occurs at a few sites in the upper Mataura, and has also been recorded from tributaries from above the Mavora Lakes in the headwaters of the Oreti River. Several aquatic snail species occur only in Southland (M. Haase, NIWA, pers. comm. 2003).

3.7.5 Stewart Island unit

The linkages between this unit and Southland during the Last Glacial Maximum have already been highlighted above, and are reflected in the similarity of their non-diadromous fish fauna—three species that occur in Southland, *Galaxias* 'southern', *G. gollumoides* and *Gobiomorphus breviceps*, also occur on Stewart Island/Rakiura (McDowall & Chadderton 1999; Waters & Wallis 2001b), but *Galaxias paucispondylus* is absent. However, the relatively early separation of Stewart Island/Rakiura as temperatures warmed presumably prevented the colonisation of the island by some common mainland families (Conoesucidae and Corydalidae: *Archichauliodes diversus*). In addition, one caddisfly species, *Traillochorema rakiura*, is known to be restricted to Stewart Island/Rakiura (Smith 2001), and stonefly communities are markedly different from those in Southland. Foveaux Strait also appears to have acted as a barrier to at least three diadromous fishes, *Cheimarrichthys fosteri*, *Galaxias postvectis* and *Gobiomorphus hubbsi*, present in mainland Southland (Chadderton 1988, 1990). A number of smaller islands are included in this unit, of which Ruapuke, Codfish Island/Whenuahau and Long Island are the largest.

4. Discussion

The biogeographic units described reflect a conceptual model of spatial variation in ecosystem character in which the distributions of species are determined by their responses to the contemporary environment and to extinction pressures exerted by major natural events in the past such as glacial maxima, volcanism and seismic activity. In many respects, the description of contemporary environmental conditions is by far the more straightforward task, as a relatively small set of environmental factors probably play a dominant direct role in structuring community composition (Snelder & Biggs 2002). In contrast, the reconstruction of the likely impacts of more distant disturbance events is much more challenging, and must be inferred either directly from physical evidence of their impacts on our landscapes, or indirectly via consideration of apparent anomalies in the distributional patterns shown by different taxa.

Fortunately, the nature of environmental changes occurring in New Zealand landscapes during the last 20 000–50 000 years has been the topic of considerable research, with numerous studies focusing on tectonism, volcanism and/or climatic change. The impacts of these major landscape-wide disturbance events on biotic distributions have been explored in only a few New Zealand studies. Doing so is made difficult by the relative lack of robust and systematically collected distribution data suitable for use in quantitative analyses that might help to unravel the relative effects of contemporary environment compared with earlier disruption events.

The patterns that emerge from the available studies and the distribution data used in this study provide important insights concerning the links between species dispersal and landscape stability. The importance of non-diadromous fish species as indicators of historic disturbance impacts is described from New Zealand (McDowall 1999) and North America (Abel et al. 2000). Many of these species exhibit sharp distribution boundaries associated with particular catchments, and these have been interpreted as reflecting the effects of volcanism in the central North Island (McDowall 1996), of glacial activity in Westland and Fiordland (Main 1989) and of tectonic movement in Southland (Waters et al. 2001).

Interaction between these relatively contemporary events and more ancient landscape features associated with tectonic movement along plate boundaries is also apparent, with ranges of mountains or hills clearly providing barriers to the dispersal of either non-diadromous fishes as a group, or to individual non-diadromous species. Specific examples include: the striking contrasts between the depauperate non-diadromous fauna of the Western South Island Province compared with the rich assemblages in eastern and southern South Island; the sharp discontinuities in individual species distributions between the Waitaki and Taieri units, separated by the Hawkdun Range and Kakanui Mountains; and the depauperate non-diadromous faunas of the Palliser–Kidnappers and Mokau units compared with those of their more inland neighbours. Similar contrasts can also be seen in the geographic separation, brought about by uplifted ranges, of pairs of closely similar species such as: *Neochanna apoda* (western South Island and lower North Island) and *N. burrowsius* (Canterbury); *Galaxias divergens* (western and northern South Island and lower North Island) and *G. paucispondylus* (eastern South Island); and *Paranephrops planifrons* (North Island and Marlborough and West Coast, South Island) and *P. zealandicus* (Eastern South Island from North Canterbury and south). While the impacts of periodic large-magnitude earthquakes are not known with certainty, they (as previously discussed) presumably had considerable potential to affect the distributions of aquatic biota through their injection of large amounts of rocky debris into water courses (Pearce & O'Loughlin 1985) and the creation of lakes (Adams 1981).

The data available for aquatic invertebrates were much more limited, consisting mostly of presence-only records of captures for individual species, with such data often problematic because of their lack of consistency in search methods and intensity of sampling. Qualitative national syntheses of such data (e.g. McLellan 1990; Collier 1993) provided invaluable supplementary information, particularly in highlighting units having unusually high levels of local endemism or pronounced shifts in community composition for particular taxonomic groups.

The techniques used for the analysis of genetic similarities between different fish populations and/or species offered some important insights for this project. Overall, however, their use was limited by the relatively small number of species and taxonomic groups that have been analysed, and the often limited numbers of geographic locations from which samples had been collected. Studies of genetic differentiation in non-diadromous fish species produced results generally consistent with the presumed historic connections between different populations (Gleeson et al. 1999; Waters & Wallis 2001b; Davey et al. 2003). By contrast, results from studies of the links between dispersal ability and genetic differentiation in invertebrate species having flying adults were ambivalent, with two studies (Smith & Collier 2001; Hogg et al. 2002) indicating an unexpected negative relationship between genetic segregation and the presumed mobility of species.

Finally, one interesting aspect to emerge was the geographic coincidence between provinces of relatively high diversity for some groups of aquatic invertebrate and/or non-diadromous fish species, and high species richness and/or endemism in terrestrial vascular plants and land snails. This was particularly apparent in the South Island, with the Otago unit exhibiting strong endemism in both vascular plants and non-diadromous fish, and northwest Nelson having high vascular plant, land snail and stonefly and hydrobiid snail diversity. Similar parallels can be seen in Northland, a centre of high diversity for both forest trees and mayflies.

5. Acknowledgements

This project was funded by DOC (science investigation no. 3538) A number of people contributed to the development of the ideas presented in this report; in particular, those who attended our 1-day workshop convened in Hamilton in October 2003. In addition to the authors, these were Richard Allibone (DOC), Mark Stevens (Massey University), Martin Haase, Bob McDowall, Ngaire Phillips and Peter Smith (NIWA), Jonathon Waters (University of Otago), and Ian Hogg and Nick Ling (University of Waikato). Their contribution of both published and unpublished data, and their comments on early drafts of this report substantially assisted the successful completion of this project. Dr M.J. Winterbourn also provided valuable comments on an earlier version of this report. Figure 1 was prepared by Chris Edkins, DOC, Wellington.

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