THE POST GLACIAL DISTRIBUTION OF NEW ZEALAND MAYFLIES

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Abstract

Situated astride the boundary of the Pacific and Austro-Indian tectonic plates, New Zealand has had a turbulent geological history. Land uplift, earthquakes and volcanism continue to the present day. Separation from Antarctica and the eastern coast of Australia in the late Cretaceous resulted in the isolation of the mayfly population. The survivors evolved into the present fauna, which includes 42 described species in 19 genera and 8 families. All species are endemic. Species distribution maps, based on more than 8,000 records included herein, illustrate a limited number of distributional patterns resulting from vegetational modification and past climatic and geological events. The results support the view that a centre of dispersal of double gilled leptophlebiid species was in northern New Zealand, but that glaciation in the south resulted in a different pattern of radiation for some single gilled Leptophlebiidae, the Nesameletidae and the Rallidentidae.
Keywords: distribution; Ephemeroptera; glaciation; interglacials; mayflies; New Zealand; Pleistocene; dispersal.

Introduction

Like those from other parts of the world, New Zealand mayflies share a tolerance of a very narrow range of environmental conditions, especially in the preadult stages. Thermal tolerance (Quinn et al. 1994), substrate size, flow rates, catchment development and its impact on water quality (Quinn and Hickey 1990, Harding and Winterbourn 1995) limit mayfly distributions. Furthermore, no New Zealand species has radiated into standing waters, except for the mayflies on the occasional rocky outcrop on a windy lake shore and in one or two lakes at the termination of glaciers.

Herein, I present distribution maps based on the results of extensive field sampling. However, it is arguable that any patterns shown are not necessarily purely the result of biogeographical processes (Hitchings 2001). Rather, they may also reflect the extent of unmodified habitat and/or intensity of collecting effort. The interpretation of such maps needs to be made with these caveats in mind.

Results and Discussion

Species Widespread Throughout New Zealand. After the end of the glacial period 14 000 bp, New Zealand became largely covered with forest (Leathwick et al. 2003, Fig. 1).

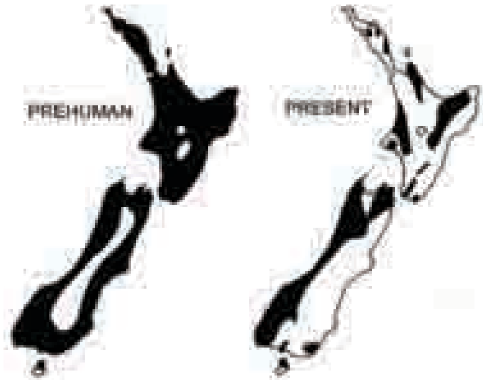

Figure 1. Forest land cover changes, prehuman and present. (Redrawn from Leathwick et al. 2003).

Before colonization by Polynesians, circa. a thousand years ago, more than four-fifths of New Zealand was forested. Now only approximately a quarter of its surface area remains covered with indigenous forest. In areas that have lost at least 90% of their forest cover, eight species of mayfly are still widely distributed. *Coloburiscus humeralis,* a filter feeder, is a typical example of this group (Fig. 2).

Figure 2. Distribution of *Coloburiscus humeralis*.

C. humeralis shows a preference for, but is not confined to, waterways flowing through forest fragments (Wisely 1962, Harding and Winterbourn 1995). It and seven other species (19%, 4 genera), not only continue to inhabit forested waterways, but have adapted to and are tolerant of conditions in areas that have been converted from forest to agricultural land or become scrub or tussock country. This group appears to be adapting well with environmental change. They could be described as winners in the stakes for evolutionary adaptation. This nucleus of common, well adapted species, has long been recognized (Winterbourn, Rounick and Cowie 1981, Rounick and Winterbourn 1982, Cowie 1985).

Table 1. Ephemeroptera species distributed throughout New Zealand, both in indigenous forest and in areas which have lost at least 90% of forest cover.

Coloburiscus humeralis	*Deleatidium myzobranchia*
Deleatidium autumnale	*Deleatidium vernale*
Deleatidium fumosum	*Neozephlebia scita*
Deleatidium lillii	*Nesameletus ornatus*

Another group of nine species (21%, 7 genera) is widely distributed on both islands, but restricted to the remaining forested regions. It seems probable their range has been reduced by habitat loss arising from the activities of the human population and its commensals.

Table 2. Ephemeroptera species whose range is now largely restricted to the remaining indigenous forest.

Ameletopsis perscitus	*Nesameletus flavitinctus*
Atalophlebioides cromwelli	*Oniscigaster distans*
Austroclima jollyae	*Oniscigaster wakefieldi*
Austroclima sepia	*Zephlebia spectabilis*
Deleatidium cerinum	

An example of a species confined to forest areas is *Ameletopsis perscitus,* the only predatory mayfly among the New Zealand fauna (Fig. 3). Its nearest relatives are *Mirawara* (Australia) and *Chiloporter* (South America).

Whatever the impact of geological uplift and planation, climate change, the rise and fall of sea levels, the advance and retreat of ice sheets and forests, the present wide distribution of these 17 species suggests an adaptability and vagility which has concealed the impact of the Pleistocene.

Figure 3. Distribution of *Ameletopsis perscitus.*

Background to New Zealand's Present Geography. The New Zealand Ephemeroptera, along with some other insect orders, are considered to have derived from old Gondwanaland forms whose vicariance came about by continental drift since the Cretaceous, circa. 80 Ma. This has been discussed elsewhere (e.g., Winterbourn 1980). The basement rocks (Fig. 4) of the western portion of the South Island derive from the late Precambrian (circa. 560 ma) to Devonian (345 Ma) Gondwana.

The remainder of New Zealand is more recent. Initially, ancestral New Zealand may have been a substantial continent, half the size of Australia. It has a very large continental shelf, however, this eroded down in the Cretaceous (136 Ma to 65 Ma) to a small low lying archipelago. Many extinctions may have taken place at this time, but conditions would also have been favorable for much speciation. New Zealand's largest genus, *Deleatidium,* a single gilled leptophlebiid, may have begun to radiate in the Oligocene, if not earlier (Fig. 5). At least six species of this genus are now widespread in both islands.

The Miocene saw continuous land, hilly but not mountainous, across a range of latitudes similar to the present (Stevens 1980). It was not until the Pliocene (2 mya) that the sea flooded across a low mid point in the alpine spine. New Zealand became separated into two main islands by a sea channel now 13 km wide at its narrowest point. Cook Strait is now a physical barrier for 17 mayfly species, 7 confined to the North Island (Table 3) and 6 to the South. For example, Cook Strait is a boundary for two species of *Ichthybotus*, a burrower sometimes considered a single genus family with nearest relatives in South America (*Euthyplocia)* (Fig. 6).

Figure 4. Basement rocks of New Zealand (in black) derived from Gondwana. (Redrawn from Coates and Cox 2002)

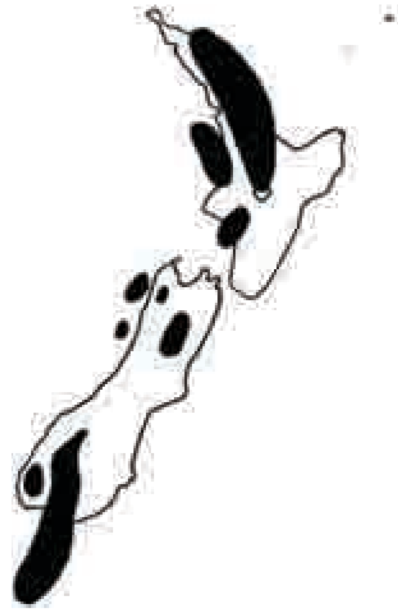

Figure 5. In the Oligocene, 35 –5 Ma, the region consisted of numerous small islands shown in black, superimposed on the present land masses. (Redrawn from Coates and Cox 2002).

Table 3. Eleven species in 9 genera restricted to the North Island, mainly in indigenous forests.

Acanthophlebia cruentata	*Isothraulus abditus*
Arachnocolus phillipsi	*Maulus aquilus*
Austronella planulata	*Tepakia caligata*
Deleatidium angustum	*Zephlebia borealis*
Deleatidium magnum	*Zephlebia tuberculata*
Ichthybotus hudsoni	

Ten leptophlebiid species were reported by Towns and Peters (1996) as restricted to the North Island and two to the South Island. In particular, the genus *Zephlebia* was richly represented in the most northern regions but much less so in the south (Fig. 7). These data confirm and refine this conclusion.

Figure 6. The distributions of *Ichthybotus hudsoni* "*" and *Ichthybotus bicolor* "•".

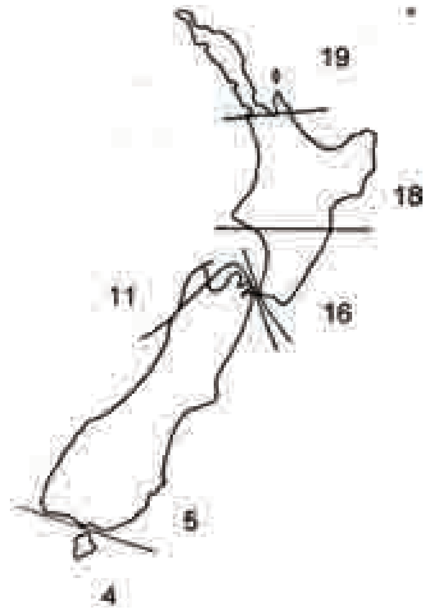

Figure 7. Variation with latitude of the number of double gilled leptophlebiid species (leptophlebiids excluding the genus *Deleatidium*).

At the time Cook Strait opened, the sea also flooded across other northern points, separating the North Island by at least two further east-west barriers to dispersal (Stevens 1980). These channels can be related, in a general way, to the present distributions of *Zephlebia* and other double gilled species. The gradation of species numbers southwards also supports the view that a centre of leptophlebiid dispersal was in the north. It has been pointed out that the close taxonomic affinities with New Caledonia, shown by some leptophlebiid species, indicate relatively recent past direct links to the north (Towns and Peters 1996, Towns and Hitchings In press).

In the early Pliocene (5–3 ma), earth movements became intense and the pattern of the present mountain ranges became apparent, extending over most of the South Island. These mountains together with smaller highlands in the central North Island were to become icebound during the glacial periods of the Pleistocene (2 ma–8 ka).

The accompanying falls in sea levels were sufficient to connect the two islands. As in the northern hemisphere, glaciers advanced and retreated several times. The seawater barrier to dispersal between the major islands was repeatedly removed and recreated. The most recent advance of glaciers, which is best understood, reached its maximum about 18 000 ya (Fig. 8). On most of the western side of the South Island, the ice sheet extended well out into the sea.

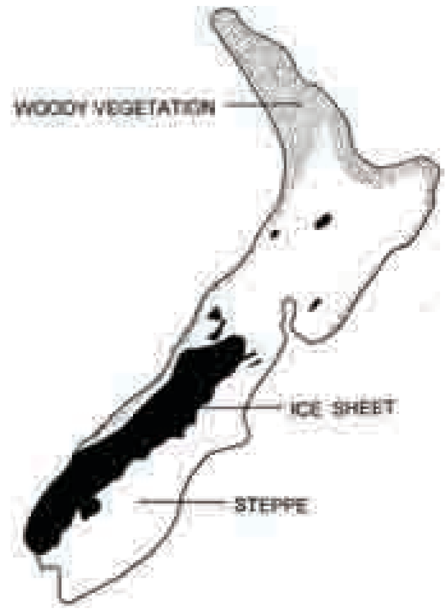

Figure 8. New Zealand 18 000 ya at its final glacial maximum and with lowered shoreline. (Redrawn from Fleming 1980).

On the eastern side much of the mountain mountain and hill country was also ice covered. During the ice advances sea levels fell to about 130 m below the present resulting in an extensive eastern coastal plain (Stevens 1980).

Some Consequences of Pleistocene Glaciation. Although almost of the North Island remained ice free, only the northwest and eastern coast of the South Island remained unglaciated. The distribution pattern shown by eight species of mayfly (Table 4) distributed in the North Island and also in the north west South Island is striking. It can be considered a consequence of the combination of lowered sea levels giving the opportunity for dispersal to the south and the ice sheet barrier confining populations to the northwest portion of the South Island.

Table 4. Eight species with North Island and N.W. South Island distributions.

Mauiulus luma	*Zephlebia inconspicua*
Rallidens mcfarlanei	*Zephlebia nebulosa*
Siphlaenigma janae	*Zephlebia pirongia* (Fig. 9)
Zephlebia dentata	*Zephlebia versicolor*

Some of these species show morphological variation between the North and South Island specimens, which may indicate incipient speciation.

Figure 9. Distribution of *Zephlebia pirongia.* Seven other mayfly species have the same distribution.

In addition to *Ichthybotus bicolor*, an additional five described species are restricted to the South Island (Table 5). Three have mountain distributions centered on the Southern Alps, one on Banks Peninsula and one on and near Stewart Island in the far south.

Table 5. Species restricted to the South Island.

Deleatidium (P) cornutum (Fig. 10)	*Nesameletus austrinus* (Fig. 10)
Deleatidium (P) insolitum	*Nesameletus murihiku*
Ichthybotus bicolor	*Nesameletus vulcanus*

Figure 10. Distributions of the South Island species *Deleatidium (Penniketellum) cornutum* "●" and *Nesameletus austrinus* "*".

Mountains can be a formidable barrier to mayfly dispersal (Edmunds 1972). There are no records in our New Zealand database of mayflies having been collected at altitudes above 1870 m. During the last glacial maximum, ice extended in the east to the edge of the plains and in much of the west, into the sea. In the east, species could only have survived in streams and rivers of coastal hills and lowlands. On the eastern South Island, such watercourses would have tended to be short, flowing more or less directly into the sea. It is feasible that isolated populations, adapted to cooler, faster water, survived in the lower reaches (Towns and Peters 1996, Staniczek and Hitchings in prep.). About 14 000 ya, retreat of the ice would have enabled some species to reoccupy the upper stretches of rivers and streams.

This has led to some interesting distributional patterns. Lowered sea levels during glacial advances linked Banks Island and Stewart Island to the mainland (Fleming 1980). Banks Island, formed from two volcanoes (12 M–6 M ya) and 80 km from the Southern Alps, was joined to the mainland by glacial outwash. Physical barriers arose during interglacial periods when sea levels rose. On Banks Island, *N. vulcanus* is considered to have speciated from the same stem species, as did the adjacent alpine species *N. austrinu* (Hitchings and Staniczek 2003).

Foveaux Strait, now separating Stewart Island from the South Island by 25 km of open sea, is shallow and became a land bridge during glacial advances.

Figure 11. Distributions of *Nesameletus murihiku* "•" and *N. vulcanus* "*".

Reestablished as an island in interglacial periods, this resulted in the speciation of *N. murihiku* from the same stem species as the now neighbouring *N. flavitinctus*. (Hitchings and Staniczek 2003).

Rallidens mcfarlanei is not a common species but it is distributed throughout the North Island and in the northwest of the South Island. A second species has been found in the east and south of the South Island (Staniczek and Hitchings In prep.). This latter may have arisen from the isolation of a population in the eastern South Island by one or more glaciations. Four relic populations exist, suggesting near extinction during glacial periods. This species seems largely confined to watercourses in foothills and plains. Apparently it was not well adapted to exploit the opportunities provided by retreat of the ice sheet.

Recently two additional *Nesameletus* species have been found in restricted parts of the Southern Alps. It will be interesting to see if their phylogenetics can be related to the changing conditions imposed on the genus by glacial advance and retreat.

I am currently addressing the problem of taxonomy and phylogenetics of the single gilled leptophlebiid genus *Deleatidium,* which contains several undescribed, cold adapted, fast water species confined to the Southern Alps.

Figure 12. Distributions of *Rallidens mcfarlanei* "•" and *R.*. sp *A* "*".

Conclusions

Pleistocene glaciation resulted in a lowering of sea levels sufficiently for the dispersal of eight species from the North into the adjacent portion of the South Island. However the southern ice fields inhibited farther dispersal. Some species, with origins in the north, including the double gilled leptophlebiids, show dispersal and distribution patterns influenced by New Zealand's former archipelagic geography.

Some species, including several single gilled leptophlebiids, restricted to the South Island, have occupied or reoccupied formerly ice covered high country. Speciation may have arisen as a consequence of isolation to restricted areas of the east coast during ice advance or rise in sea levels during interglacials.

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