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# The mayflies (Ephemeroptera) of Great Barrier Island, New Zealand: macro- and micro-distributional comparisons

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During surveys of mayfly assemblages in streams on the northern and southern blocks, Great Barrier Island, 24 species were recorded, 20 of them Leptophlebiidae. Except for the absence of Baetidae and some Siphlonuridae, this fauna is similar in size and composition to that found in forested streams at equivalent latitudes on the mainland. No endemic species were found, which, in view of the poor dispersal abilities of mayflies, indicates relatively recent continuous land links between Great Barrier and the North Island. An analysis of the mayfly fauna in relation to microhabitats on Great Barrier using a coefficient of similarity enables identification of several assemblages of species. The composition of this and other mayfly faunas reported in New Zealand is reviewed. I propose that regional variation and divergence into specific microhabitats within the Leptophlebiidae is more extensive than has been recognised previously.

*Keywords: Ephemeroptera, Leptophlebiidae, Siphlonuridae, Oligoneuriidae, streams, forest, assemblages, species richness, microhabitat.*

## INTRODUCTION

Because the immature stages of many mayflies tolerate only an extremely narrow range of environmental conditions, they can yield considerable information about the characteristics of fresh waters through responses to small changes in their immediate environment (Hubbard and Peters, 1978). In addition to the restrictive requirements of nymphs, adult mayflies do not live for more than 2-3 days (Edmunds *et al.*, 1976) and are poor fliers, traits which greatly limit their potential for dispersal (Brittain, 1982).

In theory, New Zealand mayflies should show particularly high sensitivity to environmental variations, because most species are confined to highly-oxygenated running waters. Families such as Caenidae, which elsewhere live in low flow/high temperature/low oxygen level regimes, are not found here, and the most diverse New Zealand family, Leptophlebiidae, has not radiated into the standing waters occupied by some related taxa in Australia (see Williams, 1980).

With this combination of low vagility and narrow habitat requirements, the mayfly faunas of islands around New Zealand provide a unique opportunity to investigate the effects of isolation, dispersal ability and the response of communities to reduced diversity.

Mayfly faunas of the northeastern offshore islands are particularly poorly known. In a recent review of Ephemeroptera from all northeastern islands, Wise (1983) recorded 12 taxa, 9 of them from Little Barrier Island and only one, *Acanthophlebia cruentata*, from Great Barrier Island.

Because of its relatively high elevation (up to 621 m), Great Barrier Island (28,500 ha) provides a wide range of lotic habitats compressed into small catchments. In addition, many streams have continuous forest cover from source to mouth. Depending on factors influencing the mayfly faunas, such streams could support either a low diversity of generalist vagile species or a diverse fauna with distinctive habitat requirements.

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Alternatively, barriers to dispersal and high levels of endemism in an isolated fauna may have resulted in combinations of species in ecological situations unlike those found elsewhere.

The present survey of the mayfly fauna of the northern and southern blocks of Great Barrier was undertaken with three aims in mind. First, to provide a comprehensive species list for a large island about which very little is known, and if possible to relate the composition of the fauna to the biogeographic history of the island. Second, to test rapid sampling methods required in situations of difficult access. Third, to examine the often-stated proposition that unmodified streams in New Zealand have remarkably similar faunas with a nucleus of common genera having broad ecological requirements, a suggestion which lends little support to the view that New Zealand mayflies might be expected to show high sensitivity to environmental variation. This nucleus is represented in the mayflies by *Deleatidium, Coloburiscus* and *Nesameletus* (Winterbourn *et al.*, 1981; Rounick and Winterbourn, 1982; Cowie, 1985; a, b), genera which should predominate on Great Barrier in a fauna of generalist, vagile species.

## STUDY SITES AND METHODS

Samples were obtained from 16 sites in five eastern catchments in the northern block (Fig. 1, Table 2) from 31 December 1982 to 9 January 1983. All samples but one were obtained from first order (10 cm-1 m wide) and second order (50 cm-2 m wide) streams (*sensu* Hynes, 1970). Each sample site was characterised by flow type (nil, slow, moderate or rapid) and substratum (leaves, frass, wood, gravel, bedrock). At each site as many habitats as could be identified were sampled and sorted separately. All streams flowed through mixed broadleaf-podocarp and kanuka (*Leptospermum ericoides*) forest (Wright and Cameron, 1985) and most of them had a closed or nearly closed canopy over the stream bed.

Additional collections were obtained from 14 sites in first, second and third order (1-2 m wide) tributaries of two streams at Tryphena, at the southern end of the island (Fig. 1, Table 2) in January 1984, August 1985 and January 1986. Forest cover over these streams is similar to that in the northern block, although the more northern of the Tryphena streams flows through coastal forest with a higher proportion of puriri (*Vitex lucens*) and other broadleaf species than in most of the other streams sampled (R. E. Beever, *pers. comm.*, 1984). Unlike the northern streams, which erode greywacke (Moore and Kenny, 1985), the southern block streams have a basement of andesite (B. W. Hayward, *pers. comm.*, 1984).

At each site where flow rates were low, samples of leaves, wood and frass were removed gently by hand and washed into trays. At higher flow rates, substrates were washed into a 30 × 30 cm triangular net with 0.5 mm aperture mesh. Because emphasis was on accurate determination to species level, mayflies were picked and preserved in the field, except where representative specimens were removed for rearing.

Mayflies were reared in the field in floating cages (Edmunds *et al.*, 1976) made from 6 covered plastic cups fixed into a polystyrene tray. Animals were reared to subimago in a Rangiwhakaea Bay stream, then transferred to cylindrical subimago cages (Edmunds *et al.*, 1976) for transformation to the imago.

To test the effectiveness of the general survey methods, a series of quantitative samples was obtained from the Tryphena streams. Three sites were sampled in conditions of moderate flow. At each site 10 single-stone samples were obtained from cobbles of 15-20 cm diameter (Stout and Vandermeer, 1975; Winterbourn, 1985) and all mayflies were removed and preserved. At the northern Tryphena stream samples were obtained from a forested site and in the southern stream from both forested and cleared sites.

For analysis, samples were separated according to stream order, coded by habitat and flow rate (Table 1) and each habitat within each stream tested against all others by Jaccard's Coefficient of Similarity (SJ) using a Punnet square array. This coefficient compares the presence and absence of species (e.g. Sowa, 1975), and is regarded as one of the most satisfactory indices for general use (Stark, 1985):

$$SJ = \frac{c}{a + b - c}$$

where a = the number of species at site 1
b = the number of species at site 2
c = the number of species common to both sites.

Taxonomic nomenclature follows McCafferty and Edmunds (1979) for mayfly families, Towns (1983b) for *Deleatidium* and Towns and Peters (1978, 1979a,b) and Towns (1983a) for remaining genera in Leptophlebiidae.

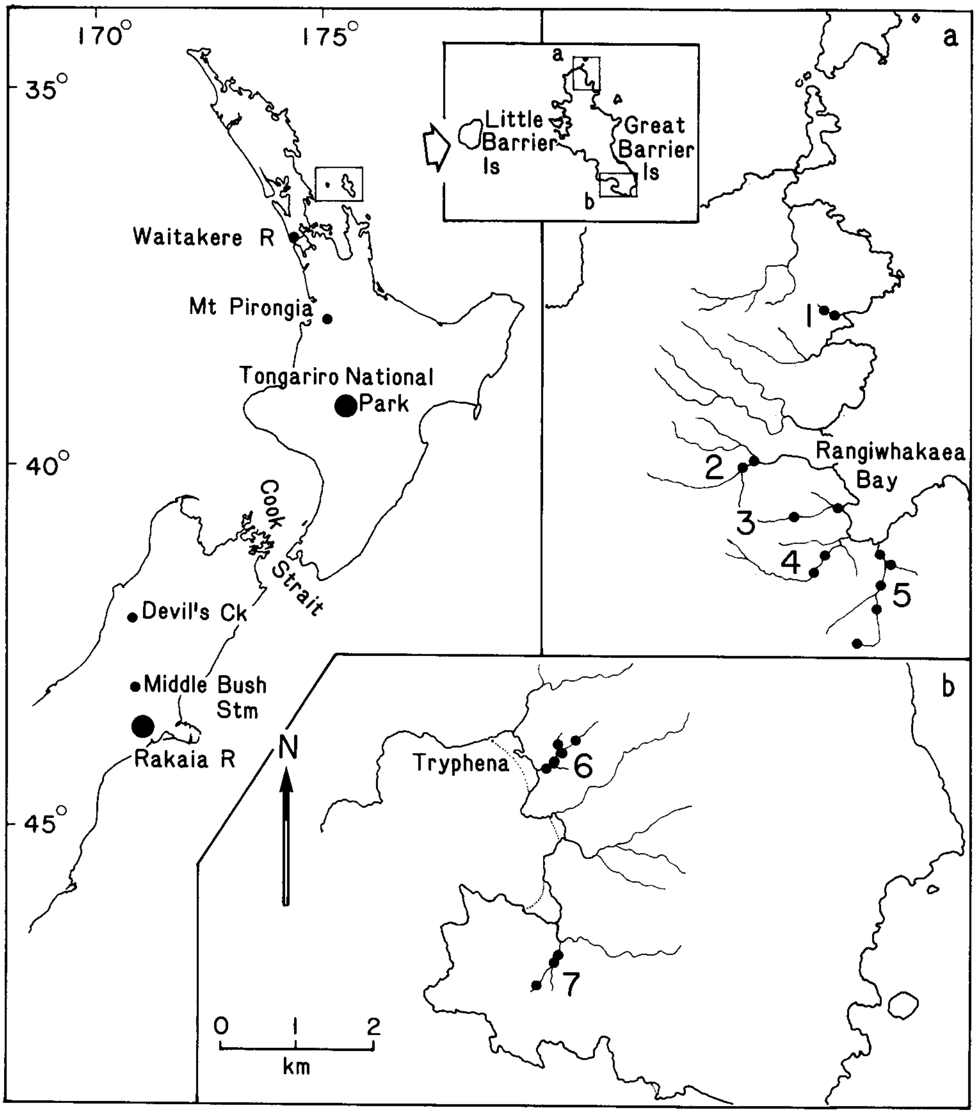


Fig. 1—Localities mentioned in the text, and locations of the catchments surveyed in the Northern (a) and Southern (b) Blocks, Great Barrier Island. Study areas in each catchment are marked (these often include >1 site) and catchments are identified as 1, Paradise Bay Stream; 2, Waterfalls Stream; 3, Slip Stream; 4, Burrill's Stream; 5, Kokako Stream; 6, N. Tryphena Stream; 7, S. Tryphena Stream. All stream names are informal; scale for a as in b.

Table 1 — Characteristics of habitats used for community comparison, Great Barrier Island.

| Punnet square code | Stream order | Flow |
|---|---|---|
| | **First** | |
| $a_1$ | Wood, frass, leaves, on gravel | nil |
| $b_1$ | Rocks, cobbles on gravel | nil to slight |
| $c_1$ | Gravel with algal film | moderate |
| $d_1$ | Waterfall/race — bedrock and pools | rapid |
| $e_1$ | Wet rock face | slight |
| | **Second** | |
| $a_2$ | Wood, frass, leaves on gravel | nil |
| $b_2$ | Rocks, cobbles on gravel | nil |
| $c_2$ | Rocks, cobbles on gravel | moderate |
| $d_2$ | Waterfalls — moss-covered bedrock | rapid |
| $e_2$ | Gravel with algal film | moderate |
| | **Third** | |
| $a_3$ | Wood on cobbles | moderate |
| $b_3$ | Rocks, cobbles on gravel | moderate |
| $c_3$ | Rocks, cobbles with algal film | moderate |
| $d_3$ | Moss-covered bedrock | rapid |

## RESULTS

Of all northern streams sampled, only "Slip Stream" showed evidence of a high level of light penetration to the stream bed, as indicated by a green film of algae over hard substrata. This stream had little forest canopy, due to a massive landslide in the headwaters which had spread down the stream bed as clay and rubble up to 2 m deep. Along the stream smashed logs and debris formed dams overlain by gravel and silt. The stream flowed beneath these obstructions, resurfacing downstream.

Other streams in the northern block showed the localised effects of smaller landslides, with large quantities of uncompacted gravel in the channels.

Many of the streams, particularly slow-flowing sections of first order tributaries, had beds carpeted with leaf material, of which taraire (*Beilschmeidia taraire*) and kanuka were predominant. At numerous places in the northern Tryphena stream, and less frequently elsewhere, leaves, twigs and other material formed substantial debris dams up to 1 m high. All streams were characterised by a paucity of bank vegetation, possibly due to grazing by feral ungulates (see Wright and Cameron, 1985), high gradient, high runoff, and short but high fluctuations in discharge. One streamside plant notable for its absence was parataniwha (*Elatostema rugosum*), the trailing leaves of which provide a habitat utilized by mayflies elsewhere (Towns, 1978b).

Twenty four mayfly species were obtained from samples collected on Great Barrier Island. The fauna was dominated by Leptophlebiidae (20 species), with other families obtained rarely, and in most samples not at all (Table 2). The siphlonurids, *Ameletopsis perscitus* and *Nesameletus* sp, were found at one and two sites respectively and the ephemerid, *Icthybotus hudsoni*, was represented by a single individual taken at a light.

Two rarely encountered species of leptophlebiid were found in large numbers at a few locations. An undescribed species of *Zephlebia* (sp A) was found on a 1 m high wet rock face in a first order tributary at Paradise Bay and in a similar situation in the southern Tryphena stream. This species has been recorded by Summerhays (1983) from Mt Pirongia and also in small runnels in the Waitakere Ranges (Towns, unpublished). The second species, *Isothraulus abditus*, known previously only from a few preserved specimens of uncertain origin (Towns and Peters, 1979b), was found in considerable numbers in an isolated pool filled with large quantities of leaves and twigs and connected to others by subterranean flow. Smaller numbers were found in first order tributaries with little discernible surface flow. These observations suggest that *I. abditus* may be most common

Table 2—Revised mayfly species list for the Waitakere River, and species composition (%) of mayflies in samples from seven catchments on Great Barrier Island. Species reared are listed +, seen but not captured, $+^{1}$; caught at lights $+^{2}$; and netted as adults, $+^{3}$. All stream names are informal.

| Species in Waitakere River | | Species on Great Barrier Island | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Paradise Bay Stm | Waterfalls Stm | Slip Stm | Burrill's Stm | Kokako Stm | N. Tryphena Stm | S. Tryphena Stm | Totals |
| **Siphlonuridae** | | | | | | | | | |
| *Ameletopsis perscitus* (Eaton, 1899) | | – | – | – | – | 0.4 | – | – | |
| *Nesameletus* sp. | | – | 2.8 | – | – | – | – | 0.9 | |
| *Oniscigaster wakefieldi* MacLachlan, 1873 | | | | | | | | | |
| *Rallidens mcfarlanei* Penniket, 1966 | | | | | | | | | |
| **Oligoneuriidae** | | | | | | | | | |
| *Coloburiscus humeralis* (Walker, 1853) | | – | 4.2 | – | 8.2 | 6.6 | – | 4.8 | |
| **Baetidae** | | | | | | | | | |
| *Siphlaenigma janae* Penniket, 1962 | | | | | | | | | |
| **Leptophlebiidae** | | | | | | | | | |
| *Acanthophlebia cruentata* (Hudson, 1904) | + $+^{2}$ | 3.2 | 7.0 | – | 16.3 | 3.1 | 2.2 | 0.6 | |
| *Arachnocolus phillipsi* Towns and Peters, 1979 | | 21.0 | 8.5 | – | – | 15.2 | 6.1 | 1.1 | |
| *Atalophlebioides cromwelli* (Phillips, 1930) | $+^{2}$ | – | 1.4 | – | + | – | – | – | |
| *Austroclima sepia* (Phillips, 1930) | | – | – | – | 28.6 | – | 10.6 | 8.0 | |
| *Austroclima jollyae* Towns and Peters, 1979 | | – | – | – | 8.2 | – | – | – | |
| *Deleatidium lillii* Eaton, 1899 | + | – | 28.2 | 8.3 | + | 10.6 | 0.6 | 2.6 | |
| *Deleatidium cerinum* Phillips, 1930 | | | | | | | | | |
| *Deleatidium myzobranchia* Phillips, 1930 | | – | – | – | – | 0.4 | – | – | |
| *Deleatidium* sp A | + | 4.8 | 11.3 | 91.7 | 20.4 | 15.6 | – | 32.2 | |
| *Deleatidium* sp C | | – | 14.1 | – | – | – | – | – | |
| *Isothraulus abditus* Towns and Peters, 1979 | | – | 2.8 | – | – | 21.1 | – | – | |
| *Mauiulus luma* Towns and Peters, 1979 | | – | – | – | – | – | (cf)3.4 | – | |
| *Neozephlebia scita* (Walker, 1853) | $+^{3}$ | – | – | – | – | 0.4 | 12.9 | 3.7 | |
| *Zephlebia (Zephlebia) versicolor* (Eaton, 1899) | | – | 4.2 | – | – | – | – | – | |
| *Zephlebia (Z.) dentata* (Eaton, 1871) | | 3.2 | 4.2 | $+^{1}$ | – | 5.1 | 27.4 | 23.7 | |
| *Zephlebia (Z.) inconspicua* Towns, 1983 | | 1.6 | 1.4 | – | 6.1 | 1.2 | 4.5 | – | |
| *Zephlebia (Z.) spectabilis* Towns, 1983 | | – | 2.8 | – | 2.0 | – | 4.5 | 4.0 | |
| *Zephlebia (Terama) borealis* (Phillips, 1930) | | 46.8 | 7.0 | – | 8.2 | 19.5 | 26.3 | 8.0 | |
| *Zephlebia* sp A | | 17.7 | – | – | – | – | – | 8.3 | |
| *Zephlebia* sp B | | – | – | – | – | – | – | 2.3 | |
| *Zephlebia* sp C | | – | – | – | 2.0 | 0.8 | 1.7 | – | |
| **Indeterminate Leptophlebiidae** | | 1.6 | – | – | – | – | – | – | |
| **Ephemeridae** | | | | | | | | | |
| *Ichthybotus hudsoni* | | – | – | – | – | – | $+^{2}$ | – | |
| SAMPLES | | 3 | 3 | 2 | 4 | 7 | 20 | 27 | 66 |
| SPECIES | | 7 | 14 | 3 | 11 | 13 | 12 | 13 | 24 |
| INDIVIDUALS | | 62 | 71 | 36 | 49 | 256 | 179 | 351 | 1004 |

in intermittent streams, a habitat in which it is encountered frequently on Little Barrier Island (K. A. J. Wise, *pers. comm.* 1985).

Except for a greater representation of Leptophlebiidae, the fauna of Great Barrier Island is similar in composition to that of the Waitakere River (Towns, 1978a) (Table 2).

Species richness was highest (14) "in Waterfalls Creek" and lowest (3) in "Slip Stream" (Table 2). Fewer species (14) were obtained from first order streams (18 samples combined) than second order streams (23 samples, 20 species), and only 13 species were taken from third order streams (23 samples). The Leptophlebiidae was the only family found in first order streams.

The Jaccard Coefficients, presented as a matrix in Table 3, show a low association between assemblages in many microhabitats. There was a perfect match (1.0) in samples from "Slip Stream" (c1, e2), where only *Deleatidium lillii* and *Deleatidium* sp A. were obtained in benthic samples (a third species, *Zephlebia dentata*, was seen but not collected). Relatively high similarity (arbitrarily defined as SJ > 0.67) was recorded when mayfly assemblages from first order streams with low flow on a gravel substratum were compared with samples in similar conditions in second order streams (b1, b2), and also when single stone samples in a forested section of the southern Tryphena stream were compared with a deforested section 100 m downstream (b3, c3).

Table 3 — Jaccard's Coefficient of Similarity for Great Barrier Island mayfly habitats (see Table 1 for codes).

| | $a_1$ | $b_1$ | $c_1$ | $d_1$ | $e_1$ | $a_2$ | $b_2$ | $c_2$ | $d_2$ | $e_2$ | $a_3$ | $b_3$ | $c_3$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $b_1$ | 0.42 | | | | | | | | | | | | |
| $c_1$ | 0 | 0.09 | | | | | | | | | | | |
| $d_1$ | 0.22 | 0.17 | 0.20 | | | | | | | | | | |
| $e_1$ | 0.18 | 0.42 | 0.29 | 0.57 | | | | | | | | | |
| $a_2$ | 0.40 | 0.54 | 0.13 | 0.10 | 0.17 | | | | | | | | |
| $b_2$ | 0.38 | 0.82 | 0.13 | 0.15 | 0.20 | 0.38 | | | | | | | |
| $c_2$ | 0.29 | 0.47 | 0.18 | 0.18 | 0.16 | 0.38 | 0.44 | | | | | | |
| $d_2$ | 0 | 0.09 | 0.13 | 0.20 | 0.29 | 0.13 | 0.18 | 0.13 | | | | | |
| $e_2$ | 0 | 0 | 1.0 | 0.20 | 0.13 | 0 | 0 | 0 | 0 | | | | |
| $a_3$ | 0.22 | 0.27 | 0 | 0.11 | 0.38 | 0.22 | 0.25 | 0.19 | 0 | 0 | | | |
| $b_3$ | 0.31 | 0.43 | 0 | 0.17 | 0.21 | 0.55 | 0.50 | 0.56 | 0.20 | 0 | 0.40 | | |
| $c_3$ | 0.13 | 0.33 | 0.20 | 0.27 | 0.55 | 0.31 | 0.40 | 0.47 | 0.20 | 0.09 | 0.40 | 0.67 | |
| $d_3$ | 0 | 0 | 0.33 | 0.40 | 0.30 | 0 | 0.08 | 0.06 | 0.33 | 0.25 | 0 | 0.08 | 0.18 |

Moderately high SJ values (>0.50<0.60) were recorded for mayfly assemblages on bedrock in first order streams with high flow (runs, falls or rock faces (d1, e1)), and when these were compared with the fauna of algal-covered cobbles in third order streams (e1, c3). Moderately high SJ values were obtained also for mayfly assemblages on gravel, rocks and cobbles in first order streams with little flow and the fauna of wood, leaves and frass in low flow, second order sites (b1, a2). Second order stream communities on a variety of substrata (leaves, wood, gravel and cobbles) also provided moderately high SJ values when compared with third order samples on cobbles (a2, b2, c2, b3).

When these results are presented as a dendrogam, using average linkage clustering (Stark, 1985), the SJ values fall into two major groups: one representing mayfly assemblages on wood, frass, leaves and gravel in slight to moderate flow and the other comprising assemblages on hard substrata with or without algae and moss cover (Fig. 2).

Within these groups are distinctive categories which contributed low SJ values in all site comparisons (Fig. 2). These were; 1, first order streams with slow flow over leaves, frass or wood (a1); 2, sites in first order streams with rapid flow over hard substrata (d1, e1); and 3, sites in second and third order streams with moderate to high flow over moss (d2, d3) (Fig. 2, Table 3).

Category a3 (wood in third order streams), although separated from other microhabitats in Fig. 2, was represented by a single sample, so its significance cannot be assessed.

The mayfly assemblages from these distinctive categories were (relative abundance over all samples in parentheses):

1. *Zephlebia borealis* (45%), *Isothraulus abditus* (29%) and *Arachnocolus phillipsi* (21%) dominating a small fauna (7 species) on wood and leaves in pools in first order streams.
2. *Zephlebia* n.sp. A (42%), *Zephlebia dentata* (19%), *Deleatidium* sp. A (16%) and *Austroclima sepia* (15%) dominating a small fauna (7 species) found on wet rock faces, runs and falls.
3. *Austroclima sepia* (72%), *Mauiulus luma* (13%) and *A. jollyae* (9%) dominating a small fauna (4 species) on moss in rapid flow.

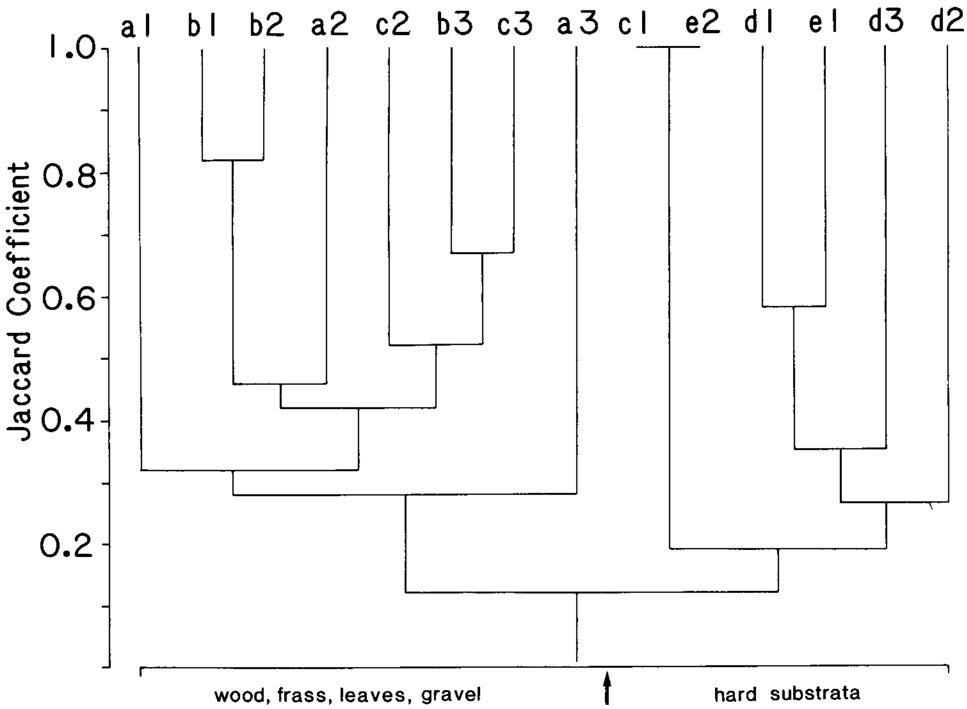


Fig. 2—Average linkage clustering dendrogram of mayfly assemblages in habitats sampled on Great Barrier Island using presence-absence data. The arrow marks the point of division between major groups (see text).

More diverse and more widely distributed assemblages included;

1. *Zephlebia borealis* (16%), *Zephlebia dentata* (14%), *Deleatidium* sp. A (13%), *Deleatidium lillii* (10%), *Arachnocolus phillipsi* (9%), *Acanthophlebia cruentata* (7%), and *Neozephlebia scita* (7%) dominating a large fauna (19 species) in low to moderate flow on wood, leaves, frass, gravel and cobbles in first and second order streams. In these habitats 8 species in the *Zephlebia* lineage (*sensu* Towns and Peters, 1980) were recorded, 6 of them in *Zephlebia* s.s.
2. *Deleatidium* sp. A (56%) and *Z. dentata* (16%) dominating a fauna (11 species) on cobbles covered with algae in third order streams.

Several species were common to more than one assemblage. However, where in one microhabitat they dominated, in another their numerical contribution was low, indicating that SJ values alone may underestimate the difference between samples. Confirmation of this was provided by comparison of the single-stone samples obtained in the two Tryphena streams. The coefficient of similarity obtained when forested sites in the two streams were compared was 0.55; the dominance sequence of the more abundant species was similar (Fig. 3); and those differences in relative abundance which did exist were only marginally significant ($X^2 = 19.84$; df = 11; $p = 0.05$). By comparison, forested and deforested sections of the same stream at Tryphena provided SJ values of 0.62, but species relative abundances which differed considerably (Fig. 3) ($X^2 = 125.53$; df = 11; $p \ll 0.01$). Invertebrate density also differed between the two sites, with significantly fewer mayflies obtained on stones within the forest ($\bar{x} = 8.5$/stone) than outside ($\bar{x} = 19.6$/stone) (Mann Whitney U Test, $z = 3.4$; $p \ll 0.01$).

The single-stone samples provided variable proportions of the fauna collected in each stream. Twelve of the 13 species (92%) identified in the southern Tryphena stream were found on stone samples, compared with only 7 of the 11 northern stream species (64%). The average number of species per stone also varied, from 2 species/stone in the northern Tryphena stream and 3 at the forested southern site, to 5 at the deforested site.

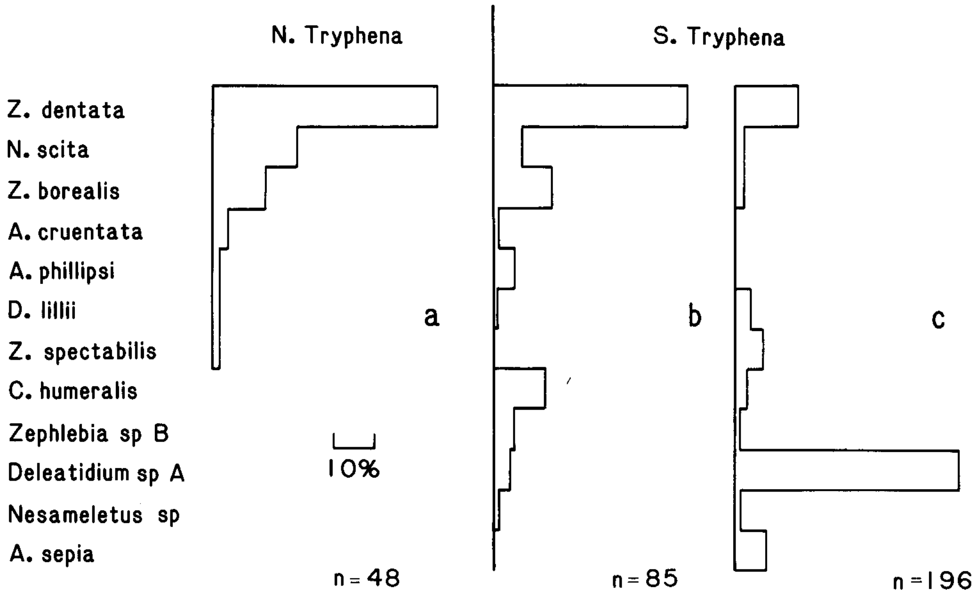


Fig. 3—Relative abundance of mayflies from single-stone samples at two forested sites (a, b) and one deforested site (c) in streams at Tryphena, Great Barrier Island.

The average number of mayfly species per stone overall (2-5) is similar to that recorded in Australia (3-5; Lake *et al.*, 1985), and temperate North America (2-9; Stout and Vandermeer, 1975) but it is not clear from overseas studies how many congeneric species shared a single stone. In southern Tryphena samples the mean number of *Zephlebia* lineage members per stone was 2 (range 0-3).

A difficulty encountered in obtaining single-stone samples is that for valid comparisons between sites each stone must be equivalently submerged. In second and third order streams this meant some selection of suitable stones was required, but in many first order streams most stones in riffles were partly exposed. Under these conditions the method is highly selective because colonizable surface area differs between stones.

## DISCUSSION

The 24 species of mayflies recorded from Great Barrier Island represent a higher species richness than was found during a recent comprehensive survey of stream faunas on Little Barrier Island (K. A. J. Wise, *pers. comm.* 1985), but is similar to that obtained at two northern North Island sites (Table 4).

Species notable for their absence from Great Barrier Island samples are the siphlonurids *Oniscigaster wakefieldi* and *Rallidens mcfarlanei* and the baetid *Siphlaenigma janae.* These are all agile, free-swimming species easily missed by unspecialised sampling methods. *Siphlaenigma* and *Oniscigaster* are both found in streams with fringing vegetation hanging into the water (Towns, 1978b; unpublished data). Elsewhere this habitat often largely comprises the perennial herb *Elatostema rugosum,* but this was absent from all streams sampled on Great Barrier Island. The same three mayfly species are unknown from Little Barrier Island (K. A. J. Wise, *pers. comm.* 1985), indicating that factors other than availability of suitable habitats might be involved. More specialised sampling on Great Barrier Island over a wider range of stream types and sizes may yet reveal their presence.

No species endemic to Great Barrier Island was found during this survey. Insects with poor dispersal abilities often show high levels of endemism where island populations have been isolated for a long time. Numerous non-aquatic examples are known from the Three Kings Islands (Ramsay and Watt, 1971), and a few are known in the Poor Knights (Watt, 1982; 1986). The mayfly faunas of Great Barrier Island and the mainland are similar,

Table 4 — Mayfly species diversity and contribution by Leptophlebiidae in a range of locations

| Location | Catchments | Altitude (m) | Vegetation | Total Species | Leptophlebiidae | Author |
|---|---|---|---|---|---|---|
| **New Zealand** | | | | | | |
| Great Barrier Is. | 7 | 2-300 | broadleaf/podocarp/kanuka | 24 | 20 | Present study |
| Little Barrier Is. | 7 | 0-150 | broadleaf/podocarp/kauri | 14 | 11 | Wise (in prep) |
| *North Island* | | | | | | |
| Waitakere R. | 1 | 20-120 | broadleaf/podocarp/kauri | 28 | 21 | Towns (1978a, unpublished) |
| Rangitukia Stm | 1 | 30-330 | broadleaf-farmland | 25 | 19 | Summerhays (1983) |
| Tongariro National Park | 14 | 750-1150 | tussock/*Nothofagus*/podocarp | 11 | 8 | Michaelis (1980) |
| *South Island* | | | | | | |
| Devil's Ck | 1 | 600-750 | *Nothofagus* | 11 | 6 | Cowie (1983) |
| Middle Bush Stm | 1 | 700 | *Nothofagus* | 3 | 2 | Winterbourn (1978) |
| Rakaia R. | 1 | 10-250 | tussock-farmland | 4 | 3 | Sagar (1986) |
| **Australia** | | | | | | |
| *Victoria* | | | | | | |
| LaTrobe R. | 1 | 55-930 | *Nothofagus*/*Eucalyptus*-farmland | 29 | 17 | Metzeling *et al.* (1984) |
| **USA** | | | | | | |
| *Florida* | | | | | | |
| Blackwater R. | 1 | 100 | conifer/evergreen/hardwood | 36 | 4 | Peters and Jones (1973) |
| **Poland** | | | | | | |
| Carpathian Mts | 6 | 158-1620 | deciduous forest-farmland | 97 | 8 | Sowa (1975) |

which suggests a recent continuous connection. Links between Great Barrier and the North Island mainland, more recent than between the North Island and the Three Kings and Poor Knights, are supported by geological evidence (Hayward, 1986). This is of particular interest because several species which are common on Great Barrier Island and in small streams in the southern North Island (e.g. *Acanthophlebia cruentata, Arachnocolus phillipsi* and *Zephlebia borealis*) are not known from the northern South Island (Towns, 1983a), even though water barriers between Great Barrier Island and the North Island, and the North Island and the South Island, apparently formed contemporaneously and now are of similar extent (Stevens, 1974; Hayward, 1986).

A distinctive feature of the mayfly fauna of Great Barrier Island, and of some sites on the North Island, is the large number of species of Leptophlebiidae and the high proportion of the fauna that they represent compared with streams outside New Zealand (Table 4), where faunas are more commonly dominated by Baetidae. Only in the Australian study of Metzeling *et al.* (1984) is proportional representation of mayfly family similar to that found in northern New Zealand, although in the Australian study the species richness of Baetidae was higher (7), and the richness of Leptophlebiidae was lower (17), than has been recorded here. In addition to the high leptophlebiid diversity on Great Barrier, four of the catchments contained 6 or 7 closely related members of the *Zephlebia* lineage. Even higher numbers (9) were found on Mt Pirongia (Summerhays, 1983) and 10 now have been identified from the Waitakere River (Towns, unpublished). By comparison, Peters and Jones (1973) recorded 5 congeneric species in both *Baetis* and *Baetisca*, and Metzeling *et al.*, (1984) obtained 6 *Baetis* species, but not more than 4 congeneric leptophlebiids. The large fauna of northern New Zealand leptophlebiids provides an unusally narrow range of life forms when compared with the large numbers of families (life forms) reported elsewhere. Add to this the restriction to highly-oxygenated running waters of most New Zealand mayflies and the fauna has the potential either to demonstrate a level of ecological divergence into specific microhabitats hitherto unrecognised, or a degree of ecological overlap rarely matched elsewhere. The community similarity analyses indicate that ecological divergence, especially in *Zephlebia*, may require further consideration. Indications of such divergence also came from Anderson (1982), who suggested that *Zephlebia* sp may be responsible for some wood degradation in streams. This is supported by the present study in which a distinctive community dominated by *Zephlebia borealis* was found on wood and leaves in first order streams. Two points mentioned earlier are relevent to these observations. First, because the composition and distribution of the leptophlebiid fauna of Great Barrier Island closely resemble that of the Waitakere River, Mt Pirongia and other sites on the northern North Island mainland (Summerhays, 1983; Towns and Peters, 1979b; Towns, 1978a; 1983b), the communities identified on Great Barrier cannot be regarded as reflecting the effects of endemism or unusual combinations of species. Second, members of the nucleus of common genera predicted by Winterbourn *et al.*, (1981), Rounick and Winterbourn (1982) and Cowie (1985a, b), regardless of stream type or riparian forest vegetation, rarely dominated the sites sampled on Great Barrier Island. Exceptions included "Slip Stream", where *Deleatidium* was abundant on eroding substrates, and the southern Tryphena stream at a deforested site. At all forested sites *Deleatidium* was less abundant than *Zephlebia*, and the other "common genera", *Coloburiscus* and *Nesameletus*, were rarely encountered.

Examination of the composition and diversity of mayfly faunas from a variety of locations throughout New Zealand suggests that regional differences could account for these apparent inconsistencies (Table 4). Of particular interest are results from the central North Island and South Island streams, where despite considerable collecting effort (e.g. Michaelis, 1980; Cowie, 1983), the number of species obtained was considerably lower than in the northern North Island or on Great Barrier Island. These regional differences may have biogeographic origins, such as the Cook Strait barrier; may be a response to hydrological features, such as stream stability and water temperature; or may reflect a combination of biogeographic and hydrological influences.

A valid criticism of regional comparisons is that sampling effort, operator efficiency and sampling methods vary between studies, making apparent differences difficult to assess. Rounick and Winterbourn (1982) recognised this when they examined a large number of streams throughout New Zealand in various types of forest and used standardised techniques. However, they obtained a surprisingly small fauna of mayflies compared with this study and those of Towns (1978b) and Summerhays (1983).

Three factors in addition to regional differences may have contributed to the lack of diversity of mayflies encountered by Rounick and Winterbourn (1982) and others. They include the way samples were obtained, the sites which were chosen and assumptions about the importance of species identification.

Stout and Vandermeer (1975) suggested that sampling uniformity can be increased to enable valid interstream comparisons by concentrating on small streams, as close to headwaters as possible, and choosing stones of 12-30 cm diameter in riffles. The various other studies in northern New Zealand indicate that small, forested headwater streams of third order or less often support the most species-rich mayfly faunas. However, restriction of samples to stone surfaces may bias samples towards the core of common genera dominated by *Deleatidium*, especially on unstable, algal-covered substrates (e.g. Sagar, 1986). Rounick and Winterbourn (1982) also suggested that it was reasonable to follow the lead of northern hemisphere workers in treating the genus as an ecological type or theme with congeneric species representing subtle variations upon it (Wiggins and Mackay, 1978), so that species-level identifications need not be important. The wide habitat divergence observed in the present study and by Summerhays (1983) indicates that this is a dangerous assumption to make when dealing with the New Zealand leptophlebiid mayflies.

Problems with species identification and the specialised sampling methods required probably have been effective deterrents to close analysis of the mayfly faunas of headwater streams in New Zealand. The simple collection and rearing methods used on Great Barrier Island enabled the identification of a diverse and interesting fauna. Comparative collections in the southern North Island and northern South Island, which concentrate on variety, rather than uniformity of microhabitats, should clarify what appear to be wide regional differences in the composition of mayfly faunas.

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