



---

## Habitat Segregation and Nymphal Life History of Two *Nesameletus* Species (Ephemeroptera: Nesameletidae) in a Mountain Stream

---

Michael J. Winterbourn

Department of Zoology, University of Canterbury, Christchurch, New Zealand

---

### Abstract

The longitudinal distribution and nymphal life history of two congeneric mayflies, *Nesameletus ornatus* and *Nesameletus* sp. A, were investigated in a New Zealand mountain stream over a period of one year. Drift and benthic samples were taken at five sites along a 380 m stretch of stream that flowed through southern beech forest upstream and tussock-grassland lower down. The two species had similar nymphal life histories with small nymphs predominating in autumn–early winter and emergence in spring and summer.

The two mayflies had strikingly different distributions with little longitudinal overlap. *N. ornatus* was confined to the three lowermost grassland sites, whereas 83% of *Nesameletus* sp. A nymphs were found in and immediately below the forest. The finding of such sharp, longitudinal habitat segregation of congeneric species over such a short distance contrasts with the observation that many New Zealand stream insects are widely-distributed habitat generalists. It is proposed that the selection of oviposition sites by females is the primary mechanism determining the distribution of nymphs within and outside forest.

**Keywords:** Ephemeroptera, *Nesameletus*, New Zealand, stream ecology, longitudinal distribution, life histories, habitat segregation.

### Introduction

Nymphs of the endemic mayfly *Nesameletus* (family Nesameletidae) are common, widely distributed members of the benthos in many New Zealand streams (Winterbourn et al., 2000). Two species (*N. ornatus* (Eaton) and *N. flavitinctus* (Tillyard) were recognised by Phillips (1930), but recent research (T. Hitchings, Canterbury Museum, pers. comm.) indicates there are at least six.

The strong-swimming, torpedo-shaped nymphs of all species are superficially similar and live in a wide range of habitats. Phillips (1930) recorded nymphs in swift currents and pools, on all sides of boulders, and on vegetation at the sides of streams. In four North Island rivers, nymphs were associated mainly with coarse substrata and in currents ranging from 0.2 to 1.5 m s<sup>-1</sup> (Jowett et al., 1991). Quinn and Hickey (1990) found they were typically members of clean-water faunas strongly dominated by mayflies and caddisflies, and the high Macroinvertebrate Community Index score of 9 (out of a possible 10) allocated to the genus (Stark, 1993) indicates a high water quality requirement. Although these observations indicate that members of the genus can tolerate a diverse range of physical conditions, a recent study by McIntosh (2002) indicates that *N. ornatus* occurs predominantly in grassland streams in the central South Island, while an undescribed species (Species A of the present paper) is found mainly in forests. A formal description of Species A is being prepared for publication in the *Fauna of New Zealand Series* (Hitchings & Staniczek, in press). Voucher specimens of both *N. ornatus* and Species A have been deposited in the Canterbury Museum, Christchurch, New Zealand.

The nymphs of *Nesameletus* are herbivore-detritivores that feed on algae and detritus by a combination of browsing and scraping (Winterbourn, 2000). In turn, they are eaten by native fish and introduced brown and rainbow trout, which influence the activity and foraging patterns of the nymphs (McIntosh & Townsend, 1994; McIntosh, 2000). Thus, *N. ornatus* nymphs taken from a fishless stream and kept in artificial channels drifted frequently during the day and night, whereas others from a trout stream were strictly nocturnal. Furthermore, the presence of predatory fish greatly reduced the amount of time nymphs spent foraging on the tops of rocks.

Few studies have considered aspects of the life cycle of *Nesameletus*, and because earlier workers were unaware that a suite of species existed, it is not always clear which species was studied. For example, in the Waitakere River system *N. ornatus* was recognized by Norrie (1969) and Rowland (1974), whereas Towns (1978) called it *N. flavitinctus*. The limited information available indicates that *Nesameletus* has a poorly synchronised, univoltine life cycle in the Waitakere River (Rowland, 1974) where its winged stages were taken in light traps in all months except July (mid-winter) (Norrie, 1969). Although extended emergence and flight periods are not unusual for stream insects in New Zealand (Ward et al., 1996; Winterbourn & Crowe, 2001), the presence of a very long flight period raises the question as to whether more than one species was present.

The finding of two species of *Nesameletus* in forested and grassland streams in the Cass-Craigieburn district of the South Island (McIntosh, 2002) led me to examine the identities of nymphs in collections of invertebrates taken by McLeod (1998) at sites along a single stream at Cass. Measurement data were then used to compare the nymphal life histories of the two species found.

## Study Stream

Middle Bush Stream is a small first-order stream on the eastern side of the Southern Alps, South Island (43°19'S, 171°46' E). It drains a 28-ha catchment supporting a

mixture of subalpine scrub, stands of mountain beech forest (*Nothofagus solandri* var. *cliffortioides* [Hook f.] Poole) and tussock-grassland. Five sampling stations were established along the stream, one in beech forest, three below the forest in mixed scrub-tussock grassland, and one further downstream in open grassland. They encompassed 380 m of stream length and were located 50–100 m apart (Fig. 1). During the

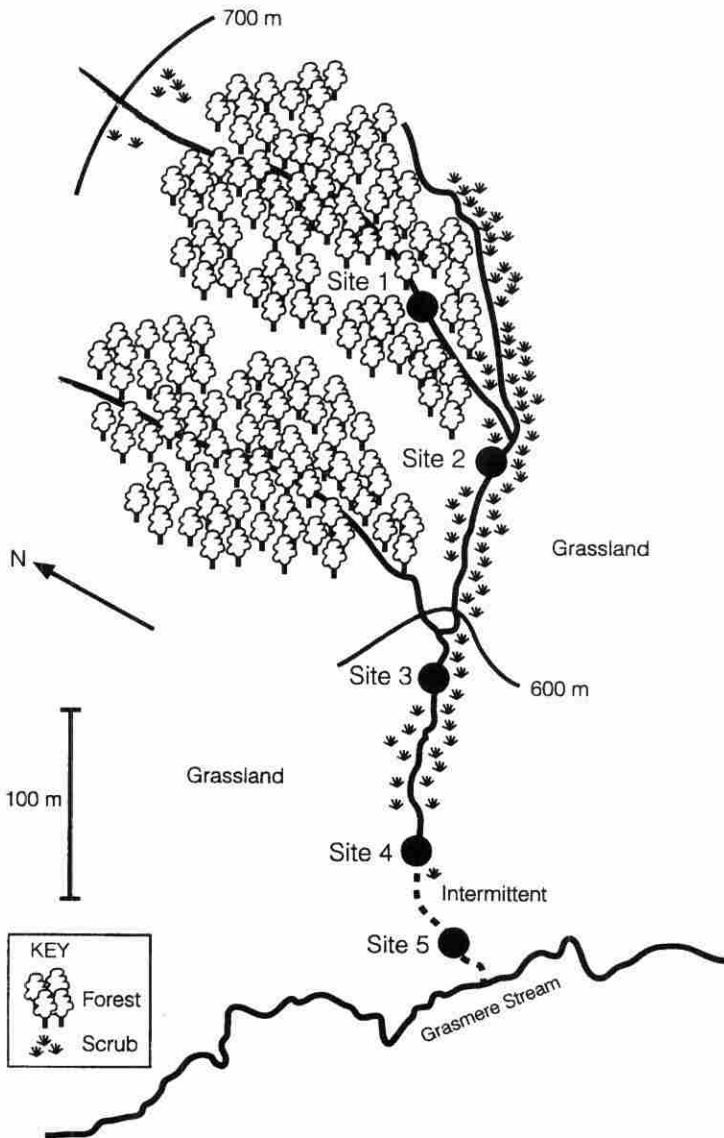


Figure 1. Map of Middle Bush Stream showing locations of the five sampling sites.

duration of the study, Sites 1–4 had permanent surface flow but the lowest site (Site 5) was dry from early February to late April 1997. Cobbles and gravels were the dominant substrata at all sites.

## Methods

Nymphs were collected at the five sites from November 1996 to October 1997. Twenty-four hour drift samples were collected each month with a sampler consisting of three nets (each net with a 105 × 55 mm opening, 1 m long, 0.25 mm mesh) positioned approximately 30 mm apart on a metal frame that was staked to the streambed. In addition, four Surber samples (0.02 m<sup>2</sup>, 0.5 mm mesh) were taken from riffles at each site in November, February, June and September. Samples were preserved in the field in 70% ethanol. No collections were made at Site 5 in February, March and April when no surface water was present.

Information on the flight periods of mayflies were obtained from a sticky trapping programme carried out concurrently at each site (Winterbourn & Crowe, 2001). Sticky traps consisted of two poly-thene sheets (one facing up- and the other down-stream; area of each sheet 0.27 m<sup>2</sup>) coated with the adhesive substance Tanglefoot®, hung across the stream channel immediately above the water. Sheets were replaced monthly when all trapped insects were removed by immersion in mineral turpentine, identified and counted.

In the laboratory preserved nymphs of *Nesameletus* were separated from samples and identified using the criteria listed in Table 1. All three characters were effective for identifying living and ethanol-preserved nymphs of all sizes. Abdomen length was used as a measure of body size. It was measured with a linear micrometer at ×10 magnification from a dark sclerotised mark at the posterior edge of the metanotal coxa to the posterior tip of the abdomen, excluding cerci and telofilum.

For site distribution and life cycle comparisons, drift and benthos data were combined.

## Results

Both species of *Nesameletus* were captured in drift and Surber samples, although they were much more abundant in the former. This is consistent with the findings of McIntosh (2002) who found that the nymphs of *N. ornatus* were difficult to sample quantitatively with benthic samplers because of their rapid swimming movements. In contrast, their behaviour may make them more prone to collection in drift nets.

### Longitudinal distribution of larvae

In total, 95 nymphs of *Nesameletus* were taken in benthos samples and 561 in drift samples. Numbers of *N. ornatus* increased downstream, abundances being highest

Table 1. Characters used to distinguish nymphs of *Nesameletus ornatus* and *Nesameletus* sp. A.

<i>ornatus</i>	Species A
Abdominal ganglia unpigmented and not visible	Abdominal ganglia dark-pigmented and prominent, ventrally
Cerci and telofilum with a broad dark bar medially	Cerci and telofilum pale with no dark bar
Each abdominal tergite with a large pale patch either side of the mid-line	Abdomen with no large pale patches, dorsally

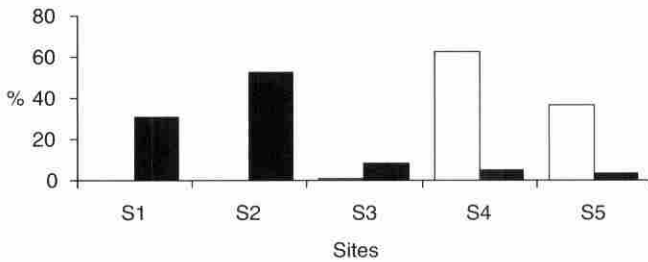


Figure 2. Relative abundance (%) of nymphs of *Nesameletus* sp. A (closed bars) and *N. ornatus* (open bars) at 5 sites along Middle Bush Stream. Based on all drift and benthic samples.

at Sites 4 and 5 (99% in both benthic and drift samples), in tussock-grassland. *N. ornatus* was not taken in or immediately below the forest at Sites 1 or 2, and its overall abundance at the intermittently flowing site (Site 5) was about half that at Site 4.

In contrast to *N. ornatus*, *Nesameletus* sp. A was most abundant in and immediately below the forest (83% in both benthic and drift samples) and very few individuals were found at the three downstream sites (Fig. 2).

### Nymphal life history

Drift and benthic sampling data were combined for life history analysis. This was considered justified since relative abundance of individuals in each 1 mm size class were not significantly different in the two largest collections of *Nesameletus* sp. A or in one of the two largest collections of *N. ornatus*. (Chi-squared goodness of fit tests,  $P = 0.28, 0.50, 0.42$ ). The exception ( $P = 0.005$ ) was where large nymphs of *N. ornatus* were over-represented in drift samples in June, possibly because their stronger swimming ability enabled them to avoid capture by the Surber sampler.

### *N. ornatus*

*N. ornatus* had a univoltine life cycle with the first very small nymph being collected in February (late summer) (Fig. 3). Large collections of nymphs obtained in April and June were dominated by small individuals, which continued to be present through winter when a wide range of size classes was present. Final-instar nymphs, subimagoes or adults were taken in small numbers from November to February. Subimagoes and adults were collected on sticky traps at Sites 3–5 where nymphs occurred each month from October to March (Fig. 4) but because they were represented mainly by wings their specific identity could not be confirmed.

### *Nesameletus* sp. A

Species A also had a moderately well synchronised, univoltine life cycle. Very small nymphs were found in April and May but by June a wide range of size classes was

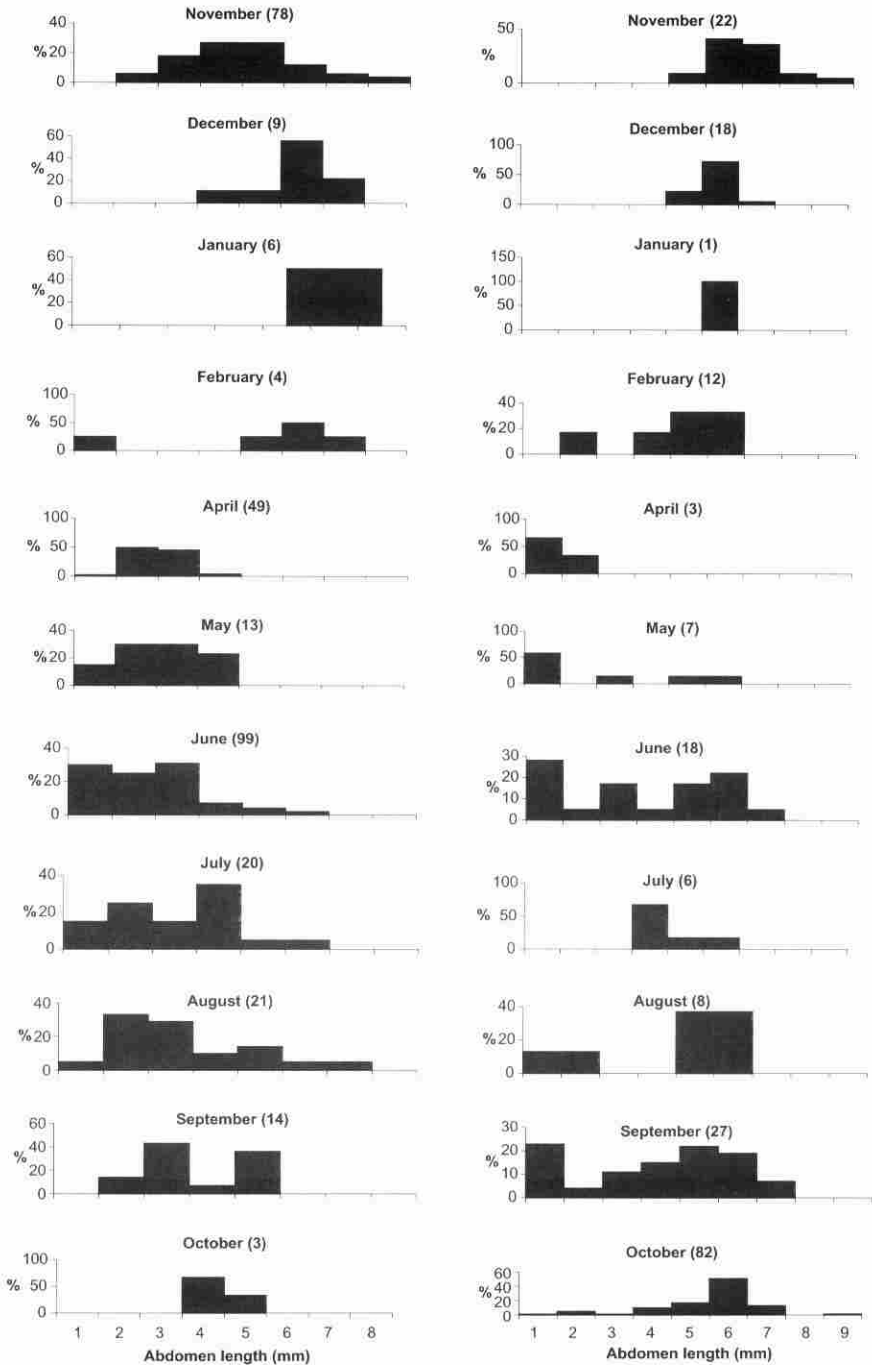


Figure 3. Life cycles of *N. ornatus* (left) and *Nesameletus* sp. A (right) based on all nymphs collected in drift and benthic samples at all sites. *n* in parentheses alongside names of the months.

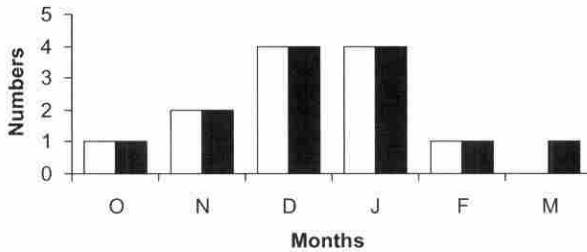


Figure 4. Combined numbers of subimagoes and adults taken each month at Sites 1 and 2 (open bars) and Sites 3–5 (closed bars). The damaged winged stages could not be identified to species, but those from Sites 1 and 2 are likely to be Species A, and those from Sites 3–5, *N. ornatus*.

present (Fig. 3). Medium–large sized nymphs predominated in October, November and December, and final instar nymphs were taken in monthly samples from September to February. Damaged adults and subimagoes were collected at Sites 1 and 2 from October to February (Fig. 4).

## Discussion

The distributions of invertebrate species along river systems are influenced by changes in physical factors such as discharge, channel width and bed sediment size, riparian vegetation, food availability and the anthropogenic modification of waterways (Naiman et al., 1987; Allan, 1995; Rice et al., 2001). They are also a function of biotic interactions and dispersal mechanisms, as well as historical factors (Carter et al., 1980; Corkum, 1992). The hydropsychid caddisflies provide several well documented examples of species replacements along river systems (e.g., Hildrew & Edington, 1979; Hauer & Stanford, 1982), while a recent study by Plague et al. (1998) indicated that three species of *Pteronarcys* (Plecoptera), occurred sequentially along a 35 km section of the Little Tennessee River. Related species of Ephemeroptera also may replace each other along river systems (e.g., *Ephemerella* species) (Culp & Davies, 1982; Ward & Stanford, 1991), although most documented examples concern patterns at scales of tens if not hundreds of kilometres. In contrast, very limited overlap in the longitudinal distributions of the two *Nesameletus* species was observed in the present study, which encompassed less than 400 m of stream. Furthermore, no nymphs of *N. ornatus*, were taken in the forested upstream reach, and the presence of a few nymphs of *Nesameletus* sp. A up to 200 m below the forest may represent downstream losses via drift from their preferred forest stream habitat.

Although some New Zealand stream insects are restricted to forested or open habitats (e.g., Cowie, 1983; Collier et al., 2000), examples of congeneric species replacing each other longitudinally at vegetational boundaries have not been reported, previously. In part, this may be because taxonomic inadequacies have prevented such

replacements being recognised, a situation that almost certainly applies to *Nesameletus* in the past. However, it also reflects the well-documented condition prevailing in New Zealand where many common stream invertebrates are habitat generalists that occur under a wide range of physico-chemical and catchment conditions (Winterbourn, 1995).

How the distribution patterns observed in the present study are maintained is not known but it is likely that the dispersal and oviposition behaviour of adult females plays a significant role in determining the distribution of nymphs. Thus, in New Zealand, McLean (1967) observed that *Coloburiscus humeralis* (Walker) oviposited in riffles where the nymphs are found, whereas *Rallidens mcfarlanei* Penniket laid eggs on the surface of pools where nymphs were most abundant. Peckarsky et al. (2000) showed that the characteristic upstream flights of *Baetis bicaudatus* Dodds females in the Colorado Rockies resulted in the colonization of headwater tributaries, while Timm (1994) demonstrated that the contrasting distributions of two *Simulium* (Diptera) species within and outside forest were determined primarily by where their eggs were laid. Since the eggs of *Nesameletus* species, like those of blackflies, are fixed to the substratum by the ovipositing female (Phillips, 1930), this behaviour is also likely to determine the primary distribution of nymphs within a stream. Of course, subsequent dispersal by active and passive means may modify the initial distribution pattern, as may interactions with conspecifics in any zone of overlap.

It is not known whether nymphs of the two *Nesameletus* species interact aggressively or compete for resources, but because their life cycles and nymphal growth patterns are similar, interspecific competition might be expected. This is especially so given Kohler's (1992) finding that competitive interactions were significant and chronic in a benthic stream community comprising many highly mobile invertebrates. In contrast, Towns (1983) found little to support the contention that competition had much effect on the composition of leptophlebiid mayfly assemblages (predominantly species of *Deleatidium*) in a northern New Zealand stream where overlap in habitat use and nymphal development periods of the species was substantial. McPeck and Brown (2000) proposed that speciation mechanisms other than the filling of empty niches (for example by differentiation of specific mate recognition systems in small populations) could account for the occurrence of speciose assemblages of *Enallagma* damselflies with very similar ecological characteristics. Such a mechanism could also be invoked to explain the sympatric leptophlebiid mayfly assemblages described by Towns. In contrast, the essentially allopatric distribution patterns of the two *Nesameletus* species considered here suggests they adapted and evolved to local ecological conditions, i.e., forest and grassland streams.

## Acknowledgements

Many thanks to Anna Crowe (née McLeod) for permission to re-examine the collections she made as the basis of her MSc thesis at the University of Canterbury.



## References

- Allan JD (1995): *Stream Ecology: Structure and Function of Running Waters*. London, Chapman and Hall.
- Carter JCH, Dadswell MJ, Roff JC, Sprules WG (1980): Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. *Can J Zool* 58: 1355–1387.
- Collier KJ, Smith BJ, Quinn JM, Scarsbrook MR, Halliday NJ, Croker GF, Parkyn SM (2000): Biodiversity of stream invertebrate faunas in a Waikato hill-country catchment in relation to land use. *N Z Entomol* 23: 9–22.
- Corkum LD (1992): Spatial distribution patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia* 239: 101–114.
- Cowie B (1983): Macroinvertebrate taxa from a southern New Zealand stream continuum. *N Z Entomol* 7: 439–447.
- Culp JM, Davies RW (1982): Analysis of longitudinal zonation and the River Continuum Concept in the Oldman-South Saskatchewan River system. *Can J Fish Aquat Sci* 39: 1258–1266.
- Hauer FR, Stanford JA (1982): Ecological responses of hydropsychid caddisflies to stream regulation. *Can J Fish Aquat Sci* 39: 1235–1242.
- Hildrew AG, Edington JM (1979): Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. *J Anim Ecol* 48: 557–576.
- Hitchings TR, Staniczek AH (in press): Nesameletidae (Insecta: Ephemeroptera). *Fauna of New Zealand*. DSIR, Wellington.
- Jowett IG, Richardson J, Biggs BJJ, Hickey CW, Quinn JM (1991): Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *N Z J Mar Freshwat Res* 25: 187–200.
- Kohler SL (1992): Competition and the structure of a benthic stream community. *Ecol Monogr* 62: 165–188.
- McIntosh AR (2000): Aquatic predator-prey interactions. In: Collier KJ, Winterbourn MJ, eds., *New Zealand stream invertebrates: ecology and implications for management*. Christchurch, New Zealand Limnological Society, pp. 125–156.
- McIntosh AR (2002): Impact of introduced trout on *Nesameletus* mayfly populations measured using electrofishing. *Arch Hydrobiol* 154: 375–392.
- McIntosh AR, Townsend CR (1994): Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology* 75: 2078–2090.
- McLean JA (1967): Studies of Ephemeroptera in the Auckland area. II: Observations on flight activity in the Waitakere Stream. *Tane* 13: 102–105.
- McLeod AL (1998): *Colonisation Pathways of an Intermittently Flowing Stream in Relation to a Changing Flow Regime and Seasonality*. MSc thesis, University of Canterbury, Christchurch, New Zealand.
- McPeck MA, Brown JM (2000): Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. *Ecology* 81: 904–920.
- Naiman RJ, Melillo JM, Lock MA, Ford TE, Reice SR (1987): Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology* 68: 1139–1156.

- Norrie PH (1969): *The Flight Activity of Ephemeroptera and Trichoptera in a Waitakere Stream*. MSc thesis, University of Auckland, Auckland, New Zealand.
- Peckarsky BL, Taylor BW, Caudill CC (2000): Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia* 125: 186–200.
- Phillips JS (1930): A revision of the New Zealand Ephemeroptera. *Trans Proc N Z Inst* 61: 271–390.
- Plague GR, Wallace JB, Grubaugh JW (1998): Linkages between trophic variability and distribution of *Pteronarcys* spp. (Plecoptera: Pteronarcyidae) along a stream continuum. *Am Midl Nat* 139: 224–234.
- Quinn JM, Hickey CW (1990): Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *N Z J Mar Freshwat Res* 24: 387–409.
- Rice SP, Greenwood MT, Joyce CB (2001): Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Can J Fish Aquat Sci* 58: 824–840.
- Rowland KE (1974): *Some Aspects of the Feeding Biology of Nesameletus ornatus (Eaton) (Insecta, Ephemeroptera)*. MSc thesis, University of Auckland, Auckland, New Zealand.
- Stark JD (1993): Performance of the Macroinvertebrate Community Index: effects of sampling method, sample replication, water depth, current velocity, and substratum on index values. *N Z J Mar Freshwat Res* 27: 463–478.
- Timm T (1994): Reasons for the shift in dominance between *Simulium (N.) vernum* and *Simulium (S.) ornatum* (Diptera: Simuliidae) along the continuum of an unpolluted lowland stream. *Arch Hydrobiol* 131: 199–210.
- Towns DR (1978): Some little-known benthic insect taxa from a northern New Zealand river and its tributaries. *N Z Entomol* 6: 409–419.
- Towns DR (1983): Life history patterns of six sympatric species of Leptophlebiidae (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution. *Hydrobiologia* 99: 37–50.
- Ward JB, Henderson IM, Patrick BH, Norrie PH (1996): Seasonality, sex ratios and arrival pattern of some New Zealand caddis (Trichoptera) to light traps. *Aquat Insect* 18: 157–174.
- Ward JV, Stanford JA (1991): Benthic faunal patterns along the longitudinal gradient of a Rocky Mountain river system. *Verh Int Verein Limnol* 24: 3087–3094.
- Winterbourn MJ (1995): Rivers and streams of New Zealand. In: Cushing CE, Cummins KW, Minshall GW, eds., *River and Stream Ecosystems*, Ecosystems of the World, Vol. 22. Amsterdam, Elsevier, pp. 695–716.
- Winterbourn MJ (2000): Feeding ecology. In: Collier KJ, Winterbourn MJ, eds., *New Zealand Stream Invertebrates: Ecology and Implications for Management*. Christchurch, New Zealand Limnological Society, pp. 100–124.
- Winterbourn MJ, Crowe ALM (2001): Flight activity of insects along a mountain stream: is directional flight adaptive? *Freshwat Biol* 46: 1479–1489.
- Winterbourn MJ, Gregson KLD, Dolphin CH (2000): Guide to the aquatic insects of New Zealand. *Bull Ent Soc N Z* 13: 1–102.

