

Life Histories of Benthic Invertebrates in a Kauri Forest Stream in Northern New Zealand

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Abstract

Life histories of the following 12 benthic invertebrate species were investigated at four sites in the Waitakere River: *Potamopyrgus antipodarum* (Gastropoda : Hydrobiidae), *Paracalliope fluviatilis* (Amphipoda : Eusiridae), *Zephlebia* (*Neozephlebia*) sp. and *Deleatidium* spp. (Ephemeroptera : Leptophlebiidae), *Hydora nitida* (Coleoptera : Elmidae), *Maoridiamesa harrisi*, ?*Austrocladius* sp. and *Paratanytarsus agameta* (Diptera : Chironomidae), *Austrosimulium australense* (Diptera : Simuliidae), *Aoteapsyche colonica* (Trichoptera : Hydropsychidae), *Oxyethira albiceps* (Trichoptera : Hydroptilidae), and *Olinga feredayi* (Trichoptera : Conoesucidae). All species had life cycles which were non-seasonal according to the Hynes model. Comparison with recent studies in southern North Island and South Island streams suggests that non-seasonal life cycles predominate in New Zealand streams.

Introduction

The benthic communities of streams draining indigenous forest catchments in New Zealand are poorly known. Most work has been limited either in time (as surveys) or in number of species studied, or restricted to groups relevant to fisheries (see Winterbourn 1978; Towns 1979). The only lotic communities for which structure and function have been investigated in detail are in mountain beech forest in the South Island (Winterbourn 1976, 1978; Winterbourn and Davis 1976; Davis and Winterbourn 1977).

This paper deals with the life cycles of 12 common benthic invertebrate species as part of a study of invertebrate communities in the Waitakere River, a stream in mixed broadleaf-podocarp and kauri forest in the northern North Island (Towns 1976, 1978a, 1978b, 1979).

Hynes (1970) classifies the life cycles of stream invertebrates into non-seasonal and seasonal types. According to this model reproduction and growth in the tropics are likely to be continuous and all life stages will be present at all times because of low annual variations in temperature and photoperiod. As a result, non-seasonal cycles will predominate. Although there are few substantive data for life cycles in the tropics, the life cycles of many stream invertebrates in the temperate Northern Hemisphere are relatively well known. At higher latitudes many species have highly synchronized life cycles, with sequential hatching and emergence of coexisting species (e.g. Plecoptera, Harper 1973), i.e. a predominance of seasonal species. The predominance becomes less apparent at lower latitudes (e.g. Ephemeroptera, Clifford *et al.* 1973), as the Hynes (1970) model would suggest.

However, although New Zealand has a temperate climate, present data suggest that many aquatic invertebrates may have non-seasonal or poorly synchronized life cycles

(Devonport and Winterbourn 1976; Winterbourn 1978). This was examined during the present study by analysis of the life cycles of a variety of common stream species. In addition, both forested and farmed sections of the stream were investigated to determine whether seasonal size distributions of the invertebrates reflect these environmental differences.

Study Area

Waitakere River is a small coastal stream on the west coast of the North Island of New Zealand (Fig. 1). Vegetation in the upper half of the catchment consists of

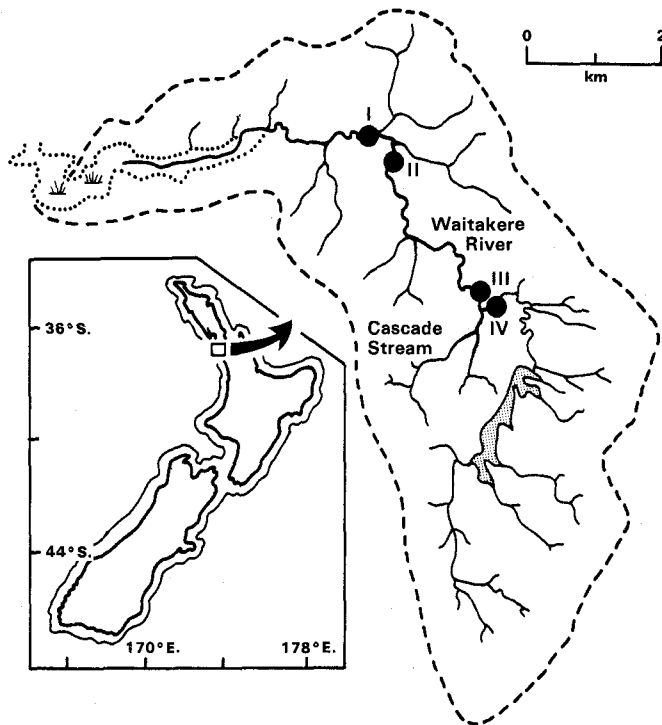


Fig. 1. Location of study area (inset), and study sites (I-IV). Waitakere River catchment area shown as a broken line.

relatively untouched mixed broadleaf-podocarp forest with large mature or regenerating stands of kauri (*Agathis australis* Salisb.). In the lower catchment the stream flows through stock-grazed scrub (including regenerating forest) and open farmed areas. Further details, including a summary of physicochemical characteristics of the stream are given in Towns (1979).

Four sites were each sampled at monthly intervals for 12 months; sites I and II were in farmland, and sites III and IV were in forest (Fig. 1). Sites III and IV had a substrate of cobbles, water depth was *c.* 10 cm and stream width *c.* 6 m. Measurable flow occurred throughout the year at all sites except site IV which was a riffle in winter and a shallow pool in summer. The substrate at sites I and II consisted of pebbles and cobbles overlying a matrix of clay (plus sand at site II). Site I was also influenced by large quantities of suspended clay, probably originating as runoff from a nearby quarry. Water depth was 10–15 cm at site II and 15–20 cm at site I. Stream width at site II was *c.* 8 m and 2–3 m at site I. Unlike the forest sites, the stream margins at sites I and II supported aquatic and semi-aquatic macrophytes. These were particularly abundant

at site I in summer, when they restricted flow to a narrow (1·5 m wide) channel. All four sites supported conspicuous periphyton growths. These were most extensive and occurred throughout the year at the farmed sites, whereas in forest areas they appeared mainly during spring and summer (November–February). Composition of the periphyton cover and its effects on the invertebrates will be discussed in a separate publication.

Materials and Methods

Each site was sampled monthly for 12 months between May 1973 and April 1974, except for site II where sampling was from July 1973 to June 1974. All samples were obtained with a 20- by 20-cm (0·04 m²) Surber sampler with a fine mesh net (200 µm aperture). Three samples were taken at each site and pooled to overcome selectivity by the sampler.

Benthic samples were preserved in 10% (v/v) formalin and later separated from gravel by the sucrose flotation method of Anderson (1959), except for cased caddis-flies which were hand-picked from sorting trays.

If more than 100 individuals were collected per site per month, specimens for life-history analysis were obtained by subsampling. Samples were placed in a glass dish on paper divided by lines 1 cm apart (0·5 mm thick) and specimens touching the lines were measured. If less than 100 individuals were obtained on the first scan, the sample was shaken and the process repeated. If used extensively this method could have produced bias towards the later instars of large species. However, this did not appear to be a problem during the present study, in which subsampling was necessary only when large numbers of early instars were present.

For life-history analyses, measurements of shell height (molluscs), body length (amphipods), head-capsule length (chironomids and simuliids), and head width across the eyes (all remaining taxa) were made with a calibrated eyepiece graticule.

Results

Fauna

During the course of the study 144 macroinvertebrate taxa were obtained in the Waitakere River system (Townsend 1978b). However, many were collected outside the sites considered here, or if present at sites I–IV, were obtained only in small numbers. Table 1 lists the 33 most abundant taxa, i.e. those representing 5% or more of the benthic standing crop at any site in any one month. Only invertebrates identified to species level are considered here. Two species of conoesucid caddis-fly, *Pycnocentrodus aeris* and *P. modesta*, although common (Table 1), are not considered because they cannot be separated as larvae (Cowley 1978).

Some identifications require comment. One species of *Zephlebia* (*Neozephlebia*) occurred in the Waitakere River, but species identification was not possible due to confused taxonomy of the subgenus. Five species at present referred to *Deleatidium* were identified from Waitakere River, of which three, *D. lillii*, *D. nr myzobranchia* and *Deleatidium* sp. C., were most abundant. *Deleatidium* sp. C. is an undescribed species near the informal 'lillii' complex of Winterbourn (1978), and *D. nr myzobranchia* may also be an undescribed species. The orthoclad chironomid *Austrocladius* sp. was extremely abundant, but despite the collection and association of larvae, pupae and adults, its generic placement remains tentative. Three species of Hydroptilidae, *Oxyethira albiceps*, *Paroxyethira hendersoni* and *P. kimminsi*, occurred at site IV in Waitakere River. Because uncased larvae of this family in New Zealand cannot be identified to species level, this stage was omitted from consideration of the life cycle of *O. albiceps* at site IV. Elsewhere, examination of pupae and cased larvae showed a predominance of *O. albiceps* and uncased larvae were assumed to belong to that species.

Table 1. Percentage contribution to benthos over 12 months by common invertebrate taxa at four sites in the Waitakere River

+ <5% present in all months; — absent. Family classification of limnephiloid caddis-flies follows Neboiss (1977), and classification of mayflies follows McCafferty and Edmunds (1979)

Taxon	Contribution (%) to benthos at site:			
	IV	III	II	I
Tricladida				
Planariidae				
<i>Cura pinguis</i> (Weiss, 1909)	3.89	—	+	+
Nemertea				
Tetrastemmatidae				
<i>Prostoma ?graecense</i> (Bohming, 1898)	1.40	+	1.17	+
Annelida				
Lumbricidae				
<i>Eiseniella tetraedra</i> (Savigny, 1826)	+	—	+	0.39
Phreodrilidae				
<i>Phreodrilus</i> sp.	1.36	+	—	—
Naididae				
<i>Slavina appendiculata</i> d'Udekem, 1855	19.22	5.24	+	4.96
Mollusca				
Hydrobiidae				
<i>Potamopyrgus antipodarum</i> (Gray, 1843)	5.51	5.62	28.64	52.13
Crustacea				
Cyclopidae				
<i>Macrocylops albidus</i> (Jurine, 1820)				
+ <i>Acanthocylops robustus</i> (G.O. Sars, 1863)	3.45	+	+	+
Eusiridae				
<i>Paracalliope fluviatilis</i> (Thomson, 1879)	—	—	—	17.37
Insecta				
Oligoneuriidae				
<i>Coloburiscus humeralis</i> (Walker, 1853)	+	2.34	0.25	+
Leptophlebiidae				
<i>Zephlebia</i> (<i>Neozephlebia</i>) sp.	1.55	7.12	+	+
<i>Zephlebia</i> (<i>Zephlebia</i>) sp.	1.88	+	+	+
<i>Deleatidium lillii</i> Eaton, 1899	2.62	13.87	0.97	+
<i>Deleatidium</i> nr <i>myzobranchia</i> Phillips, 1930	+	2.65	0.50	+
<i>Deleatidium</i> sp. C	0.54	2.47	+	+
Leptophlebiids (undetermined)	1.71	11.09	2.48	+
Gripopterygidae				
<i>Acroperla trivacuata</i> (Tillyard, 1923)	—	+	+	0.62
<i>Zelandobius furcillatus</i> Tillyard, 1923	+	+	0.43	+
Corydalidae				
<i>Archichauliodes diversus</i> (Walker, 1853)	+	2.14	+	+
Elmidae				
<i>Hydora nitida</i> Broun, 1885	17.93	6.75	14.46	2.26
Tipulidae				
Limoniini sp.	+	+	0.40	+
Chironomidae				
<i>Maoridiamesa harrisi</i> Pagast, 1947	—	+	1.10	0.15
? <i>Austrocladius</i> sp.	2.05	2.22	9.17	2.61
<i>Cricotopus zealandicus</i> Freeman, 1959				
+ <i>Syncricotopus pluriserialis</i> (Freeman, 1959)	+	+	1.07	+
<i>Paratanytarsus agameta</i> (Forsyth, 1971)	3.90	7.48	3.36	0.50

Table 1 (Continued)

Taxon	Contribution (%) to benthos at site:			
	IV	III	II	I
Simuliidae				
<i>Austrosimulium australense</i> (Schiner, 1868)	+	+	1.11	0.40
Hydropsychidae				
<i>Aoteapsyche colonica</i> (McLachlin, 1871)	+	2.30	4.16	+
Hydroptilidae				
<i>Oxyethira albiceps</i> (McLachlin, 1862)	+	0.78	6.45	6.59
<i>Paroxyethira kimminsi</i> Leader, 1972	0.82	+	—	—
Conoesucidae				
<i>Beraeoptera roria</i> Mosely, 1953	+	0.63	+	+
<i>Pycnocentroides aeris</i> Wise, 1958				
<i>Pycnocentroides modesta</i> Cowley, 1976	12.71	7.46	12.94	2.85
<i>Olinga feredayi</i> (McLachlin, 1868)	3.41	6.54	+	+

Potamopyrgus antipodarum

The hydrobiid snail, *Potamopyrgus antipodarum*, was one of the most widespread species collected during the study and at site I dominated the samples (Table 1).

Monthly size distribution varied greatly between sites (Fig. 2). First influx of newly released young (0.5 mm) occurred in October at sites II–IV, but in November at site I. Thereafter, the 0.5-mm group showed a decline in its representation in three of the four populations. At site I, however, a second influx of young occurred in April. At site III, unlike the other areas, there was a continuous strong bias towards the smallest size group from October to March (spring and summer) (Fig. 2), with the virtual absence of females with embryos (three in 12 months sampling). The predominance of very small snails at this site was probably the result of constant recruitment of newly hatched individuals from outside, and high mortality (or loss) rate. In contrast, the two lower sites had a higher proportion of egg-carrying adults. The largest resident population of mature females occurred at site I.

Growth rates were relatively clear for the population at site I, and monthly size-frequency data suggest that it consisted of two overlapping growth cohorts (Fig. 2). Young released in November reached maturity (3.5 mm) in 4 months, and possibly released their first embryos in April (5 months). Young released in April grew slowly during winter to reach maturity the following October or November (7 months). In addition, small numbers of embryos were released almost continuously. A similar summer growth pattern occurred in the population at site IV, but in contrast with site I, there is no evidence that *P. antipodarum* produced two complete generations per year.

Paracalliope fluviatilis

Two species of eusirid amphipod were obtained during the present study. The phreatic *Paraleptamphopus subterraneus* was found only in a minor tributary, while the more common *Paracalliope fluviatilis* was often abundant in the lower Waitakere River at site I (see also Towns 1979).

Small amphipods were most common in November, although they occurred in the samples from October to April. Fully developed young *P. fluviatilis* were occasionally found while still in the marsupium. The few obtained averaged 0.32 mm in length (range 0.24–0.40 mm, $n = 6$). Free-living amphipods of this size were obtained only

in November, although slightly larger individuals were present for most of the year. This, and the presence of ovigerous females in samples each month, indicate that *P. fluviatilis* is sexually active throughout the year (Fig. 3). Size-frequency analysis (Fig. 3) suggests that young released in spring (October, November) potentially were able to produce their first clutch in March (late summer).

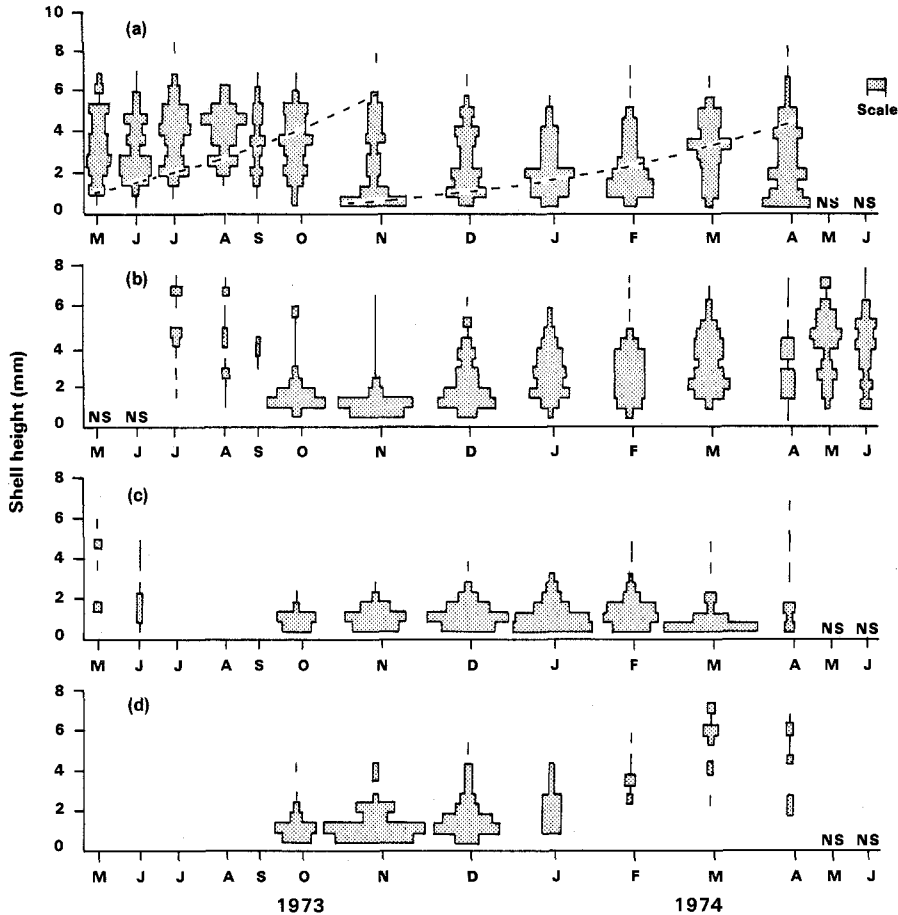


Fig. 2. Monthly size distribution of *Potamopyrgus antipodarum* in the Waitakere River at sites I(a), III(c), IV(d) from May 1973 to April 1974 and at site II(b) from July 1973 to June 1974. Scale: 10 individuals. ——— Suggested growth cohorts. In Figs 2–14, size distributions plotted only where >5 specimens obtained. NS, no sample. Sample sizes: site I, $n = 1246$; site II, $n = 829$; site III, $n = 543$; site IV, $n = 370$.

The smallest ovigerous females were 1.4 mm total length (except for a single individual of 1.2 mm). Clutch size ranged from one to eight, with most females carrying two, three or four young. Mean clutch size was 3.11 (s.d. = 1.42, $n = 120$), a slight underestimate as some amphipods lost part of their clutches following preservation.

Unlike most amphipods which couple with males grasping females by the dorsum (Bousfield 1973), *P. fluviatilis* apparently in precopula invariably paired side by side. As with many freshwater amphipods, coupled pairs of *P. fluviatilis* consisted of a large male and smaller female. Of 20 pairs measured in precopula, only once was the male

smaller than the female (size of females ranged from 1.6 to 2.6 mm and males from 2.1 to 3.4 mm). Because females carrying young were found in precopula, they are apparently capable of producing several batches of eggs in succession.

Zephlebia (Neozephlebia) sp.

Like most mayfly species from the four main study sites on Waitakere River *Zephlebia (Neozephlebia) sp.* was most abundant at site III (the only site from which specimens were taken in all months). This indicates that at sites I, II and IV populations were transient and recruited from outside the immediate area, a suggestion supported by the disjunctive size distributions of their *Zephlebia (Neozephlebia) sp.* populations (Fig. 4).

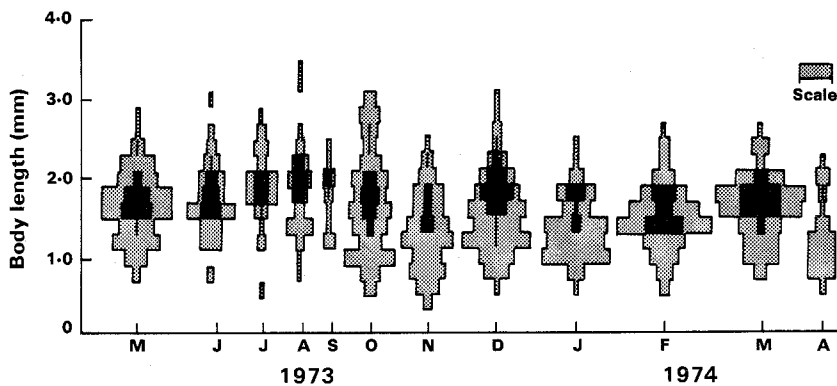


Fig. 3. Monthly changes in abundance of *Paracalliope fluviatilis* at site I in the Waitakere River: $n = 902$. Dark shading represents ovigerous females. Scale: 10 individuals.

The size-frequency data suggest two alternative interpretations of the life history of *Zephlebia (Neozephlebia) sp.* The species may have one generation per year, with extensive and delayed hatching and emergence strongest in spring but continuing through summer as the next generation appears. Alternatively, there may be two emergence cohorts per year, one arising from the rapid growth of nymphs hatching in late winter and growing to emerge in autumn, and a second, and more numerous, generation appearing from nymphs hatching in summer and emerging the following spring.

Deleatidium spp.

Deleatidium spp. nymphs were most abundant at site III where *D. lillii* predominated, but *Deleatidium sp. C* and *D. nr myzobranchia* also were seasonally abundant. At the remaining sites only small numbers of *Deleatidium spp.* nymphs were obtained (mostly *D. lillii*).

For seasonal size distribution of *Deleatidium spp.* nymphs (Fig. 5) all species have been combined. However, since *D. lillii* dominated most samples, Fig. 5 largely reflects the life history of this species. The marked influx of small nymphs in summer was similar to that found for *Zephlebia (Neozephlebia) sp.* It is notable that *Deleatidium spp.* nymphs were rare at sites I and IV during late summer when early instars were abundant at sites II and III. This is similar to results obtained for *Zephlebia (Neozephlebia) sp.* and suggests that summer conditions were not suitable for the genus

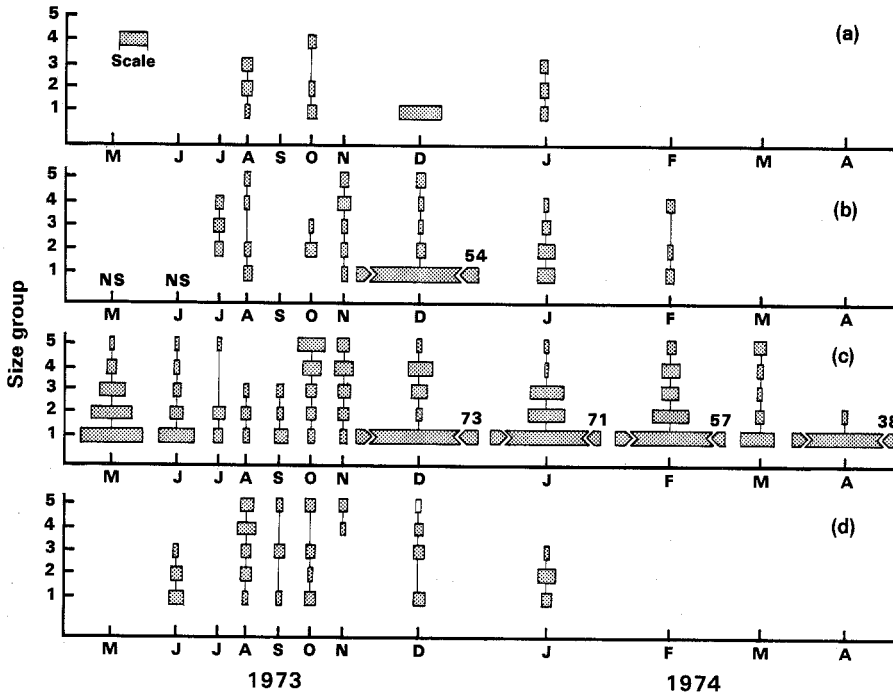


Fig. 4. Monthly size distribution of *Zephlebia* (*Neozephlebia*) sp. at sites I(a), II(b), III(c) and IV(d) in the Waitakere River. Head-width measurements for size groups: 1, <0.6 mm; 2, 0.6–0.8 mm; 3, 0.8–1.0 mm; 4, 1.0–1.2 mm; 5, >1.2 mm. Sample sizes: site I, n = 42; site II, n = 121; site III, n = 541; site IV, n = 86. Scale: 10 individuals.

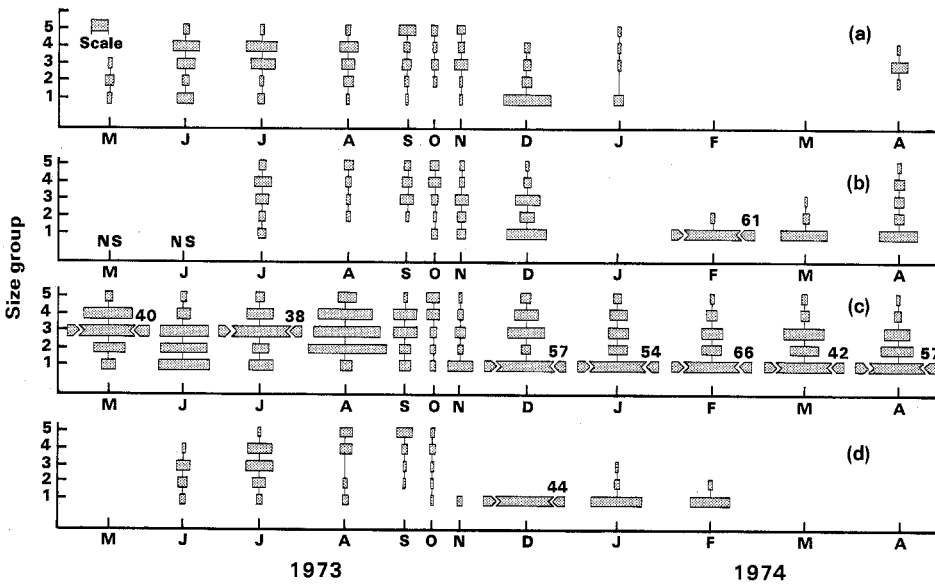


Fig. 5. Monthly size distributions of *Deleatidium* spp. at sites I(a), II(b), III(c) and IV(d) in the Waitakere River. Head-width (HW) and wing-bud (WB) measurements for size groups: 1, HW <0.6 mm; 2, HW 0.6–0.8 mm; 3, HW 0.8–1.2 mm; 4, HW >1.2 mm, WB <1.6 mm; 5, HW >1.2 mm, WB >1.6 mm. Sample sizes: site I, n = 332; site II, n = 427; site III, n = 1123; site IV, n = 228. Scale: 10 individuals.

at sites I and IV. As a result, the life cycles were effectively truncated at the time of year when hatching recruitment was normally maximal.

Size-frequency distribution at all sites showed a tendency for maximum hatching in summer, and most last instars were present in late winter and spring. However, very small nymphs (head width <0.6 mm) were present throughout the year (Fig. 5).

Hydora nitida

Larvae identified by association with adults as *Hydora nitida* (see Towns 1978b) were common in all samples from sites I to IV.

Adults were obtained with larvae in benthic samples during spring and summer. A curious feature of the adult monthly distribution was their appearance at sites III and IV a month later than at the two downstream sites. In both areas adults were captured for 4 months, from November to February at sites III and IV and from October to January at sites I and II.

An attempt to divide collections of *Hydora nitida* larvae into size cohorts corresponding to instars by probability paper analysis (Cassie 1963) was unsuccessful. However, head-capsule widths (Fig. 6) provided a clear indication of the larval life cycle from sites II, III and IV. First appearance of small larvae occurred approximately a month after first capture of adults (except at site I) and continued while adults were present. Hatching was therefore concentrated around December, January and February, but early instars continued appearing in small numbers until April (site II). Growth continued slowly over winter and more rapidly over summer, with larvae approaching their largest size in their second winter. This produced a bimodal distribution, particularly obvious at site II from December to June (Fig. 6). It is probable that larvae leave the stream to pupate some time in their second winter and emerge as adults in spring and early summer. Therefore the total development period from hatching to flight would be approximately 23 months.

Maoridiamesa harrisi

In Waitakere River, the chironomid *Maoridiamesa harrisi* (Diamesinae) did not occur at site IV and was rare at sites I and III, but was often abundant at site II during winter and spring.

Head-capsule length analysis suggests four larval instars, the normal number for Chironomidae (Oliver 1971). Instars 3 and 4 were most common in the samples (Fig. 7), although net aperture was small enough to retain all chironomids down to and including instar 2. Possible explanations for the bias are rapid growth through the first instars, followed by slower growth of instars 3 and 4, or alternatively the occurrence of only later instars in riffle habitats. In Chironomidae the first instar is commonly the main dispersal phase (review by Davies 1976) and these may have been more abundant in pools or along stream margins.

The life cycle of *M. harrisi* is difficult to interpret. Even though the predominance of last instar individuals may be indicative of rapid growth to maturity, it remains uncertain whether single or multiple generations are represented.

?*Austrocladius* sp.

The orthoclad *Austrocladius* sp. was the most abundant Waitakere River chironomid and occurred at all sites.

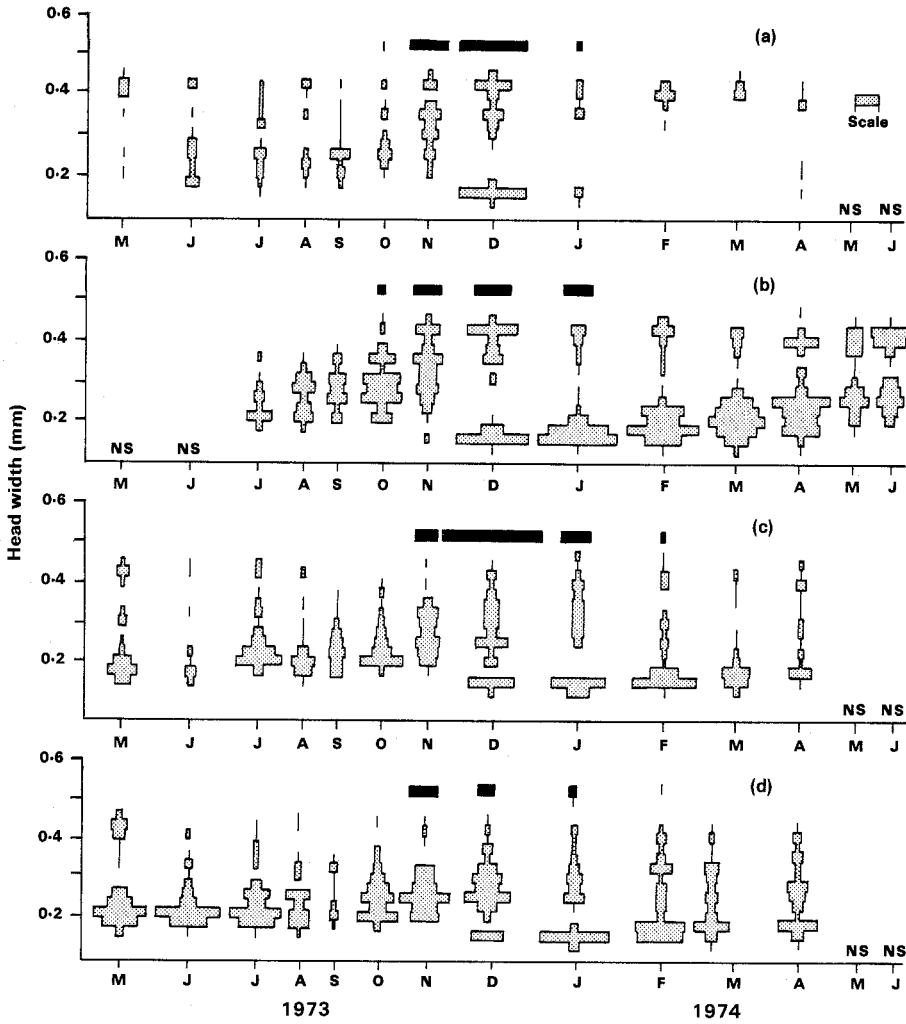


Fig. 6. Monthly size distribution of *Hydora nitida* larvae (pale shading) and adults (dark shading) at sites I(a), II(b), III(c) and IV(d) in the Waitakere River. NS, no sample. Sample sizes: site I, $n = 334$; site II, $n = 1001$; site III, $n = 630$; site IV, $n = 887$. Scale: 10 individuals.

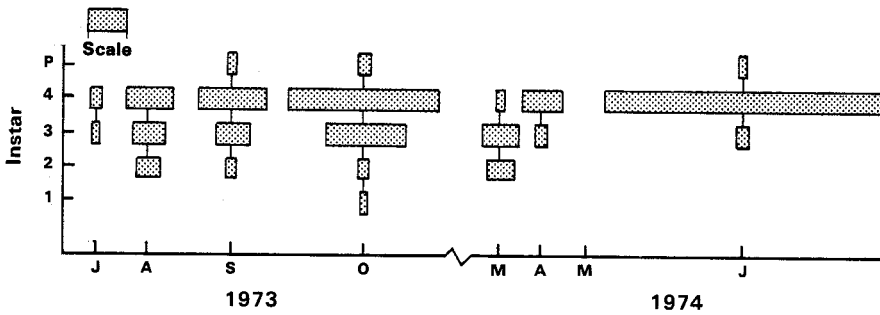


Fig. 7. Monthly instar distribution of *Maoridiamesa harrisi* larvae at site II in the Waitakere River; $n = 218$. Head-capsule lengths of suggested instars: 1, 0.13 mm; 2, 0.20–0.30 mm; 3, 0.33–0.45 mm; 4, 0.50–0.80 mm. Scale 10 individuals.

Because there were no breaks in head-capsule length frequency, instar analysis was not possible. This was also confused by the presence of at least two other unidentified species with larvae of similar size and appearance to those of *Austrocladius* sp., and early instars of the larger orthoclad species *Cricotopus zealandicus* and *Syncricotopus pluriserialis*.

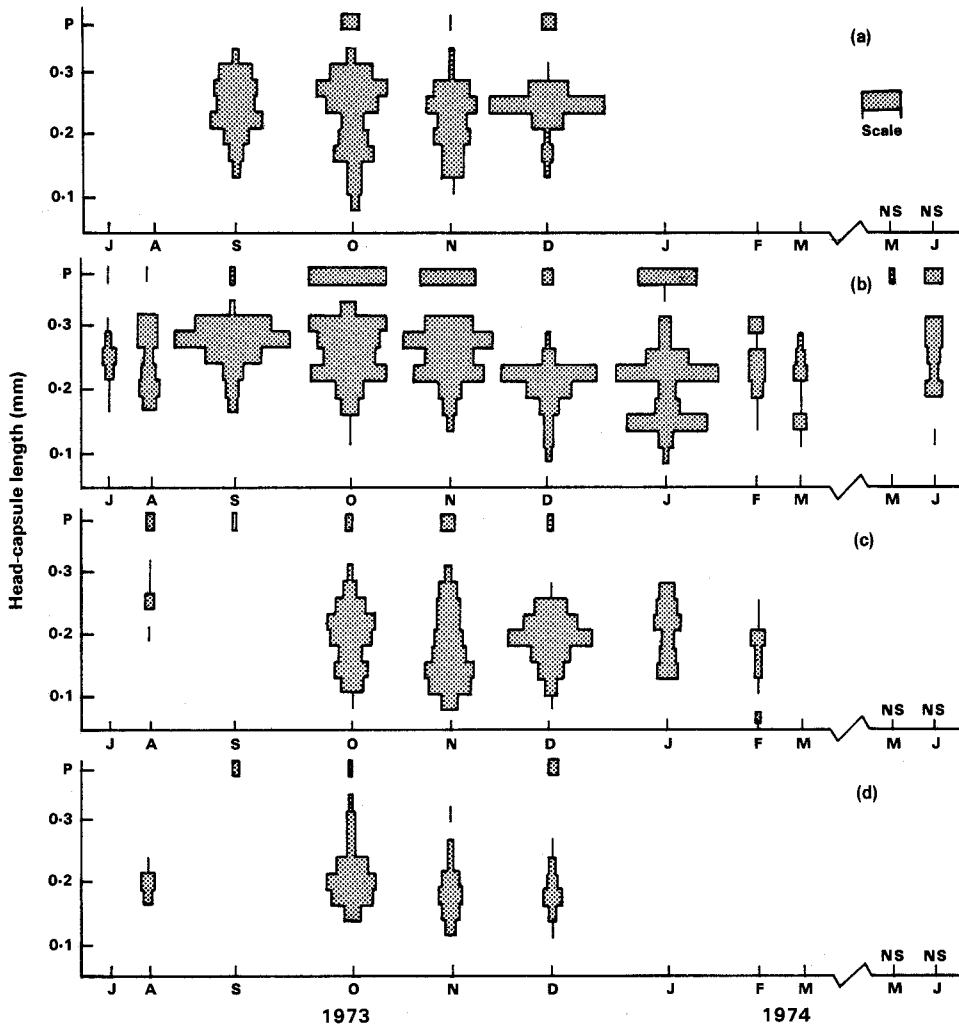


Fig. 8. Monthly size distributions of *Austrocladius* sp. larvae and pupae at sites I(a), II(b), III(c) and IV(d) in the Waitakere River. NS, no sample. Sample sizes: site I, $n = 291$; site II, $n = 546$; site III, $n = 273$; site IV, $n = 103$. Scale: 10 individuals.

Ungrouped head-length measurements were used in an unsuccessful attempt to interpret the annual cycle of this species (Fig. 8). However, the presence of pupae at most times when larvae were captured, even following months when larvae were rare (Fig. 8), suggests that *Austrocladius* sp. has rapid development and is probably multivoltine.

Paratanytarsus agameta

Larvae of this species of Chironominae were common in the Waitakere River where largest numbers occurred in spring and summer at site III.

Unlike *Austrocladius* sp., *P. agameta* head-capsule lengths fell into reasonably discrete size groups, although they showed some overlap. Breaks between groups were obtained by probability paper analysis (Cassie 1963). The three resulting size classes probably represent instars, the smallest group being a combination of instars 1 and 2 (Fig. 9).

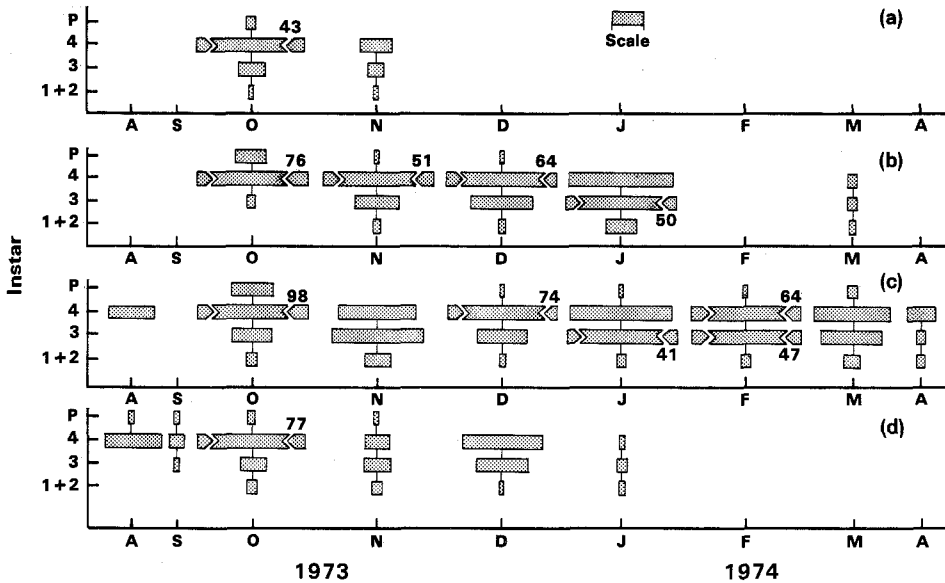


Fig. 9. Monthly instar distribution of *Paratanytarsus agameta* larvae and pupae at sites I(a), II(b), III(c) and IV(d) in the Waitakere River. Head-capsule lengths of suggested instars: 1 + 2, <0.15 mm; 3, 0.15-0.25 mm; 4, 0.25-0.38 mm (n = 1180). Sample sizes: site I, n = 69; site II, n = 356; site III, n = 562; site IV, n = 199. Scale: 10 individuals.

As for *Austrocladius* sp. and *Maoridiamesa harrisi*, the greatest numbers of *P. agameta* larvae captured belonged to the final instar. Analysis of instar composition of *P. agameta* by month and site showed that pupae generally were present at any time that larvae were abundant (Fig. 9). This probably indicates rapid development, as found by Forsyth (1971) for a laboratory population of *P. agameta* which had an average generation time of 17 days at 20°C.

Austrosimulium australense

Larvae of the simuliid *A. australense* constituted a major portion of the fauna at each site during spring, particularly at the two downstream sites.

Instars could not be differentiated using head-capsule length, so larvae have been placed for convenience into four size groups (Fig. 10) based on abundance peaks in the size-frequency distribution.

Larvae were not present in large enough numbers or for a sufficiently long period for any growth pattern to be distinguished, and very few pupae were obtained. Like chironomids, however, the largest *A. australense* size group was present in most

samples (Fig. 10). Individuals in the largest size group included specimens with head lengths of 0.68–0.75 mm and darkened respiratory histoblasts indicative of the last larval instar (Crosby 1974).

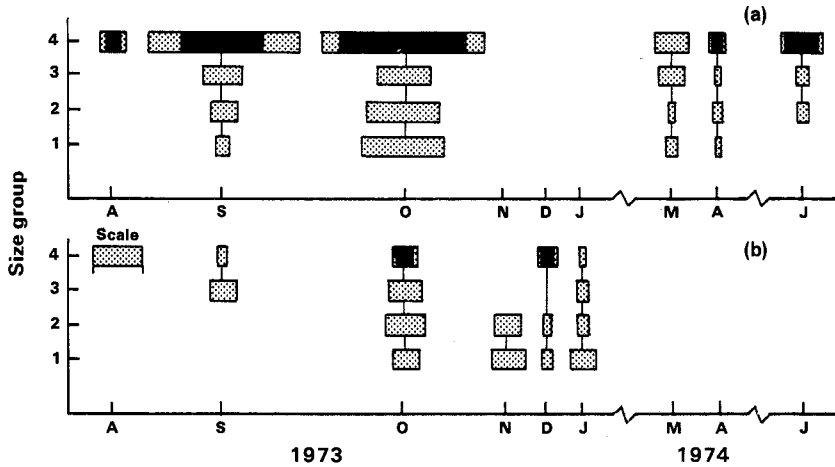


Fig. 10. Seasonal size distribution of *Austrosimulium australense* larvae at sites II(a) and III(b) in the Waitakere River. Larvae with darkened respiratory histoblasts are shaded. Head-capsule lengths of size groups: 1, 0.15–0.33 mm; 2, 0.35–0.45 mm; 3, 0.48–0.58 mm; 4, 0.60–0.75 mm ($n = 332$). Sample sizes: site II, $n = 168$; site III, $n = 66$. Scale: 10 individuals.

Aoteapsyche colonica

The hypsopsychid caddisfly *A. colonica* was common at sites II and III.

Instars have been separated by head-capsule measurements of larvae collected over 12 months (May–April) at the four sites. Because instars 1–3 overlapped in size, breaks between them were estimated by probability paper analysis. The size range for each instar approximates the values of Crosby (1975) (Fig. 11). However, Crosby

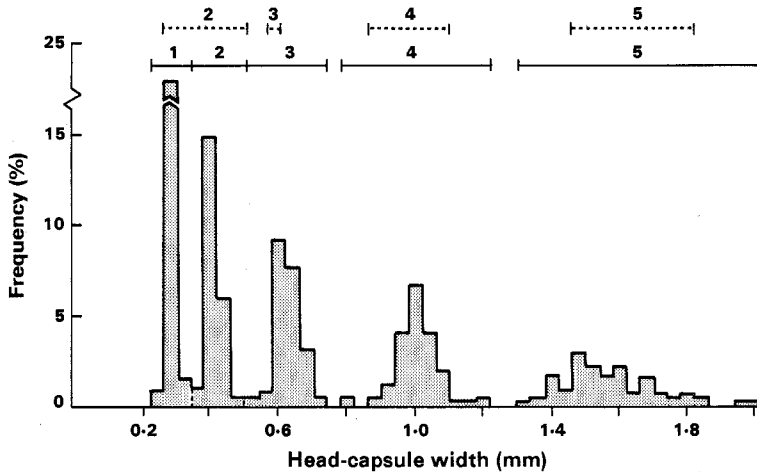


Fig. 11. Frequency distribution of head widths of *Apteapsyche colonica* larvae with suggested instars (—) and those of Crosby (1975) (---) numbered; $n = 954$.

considered that his smallest size group represented instar 2 and that first-instar larvae were not captured. My analysis suggests that his 'second instar' actually included instar 1.

From analysis of monthly size composition (Fig. 12), larvae appearing as first instars in October at site III would probably reach the fifth instar in April, a larval life of 6–8 months. Similarly, the data provided by Hopkins (1976) suggest a larval life of 6–10 months.

The relatively clear growth pattern found in Waitakere River at site II differs from that at site III. This may be due to movement of first-instar larvae out of site III in spring but not in summer in response to availability of prey.

The continued appearance of first instars at both sites, and the presence of fifth-instar larvae in most months (10 out of 12 months at site III, every month at site II) (Fig. 12), suggest that *A. colonica* is able to hatch and emerge throughout the year.

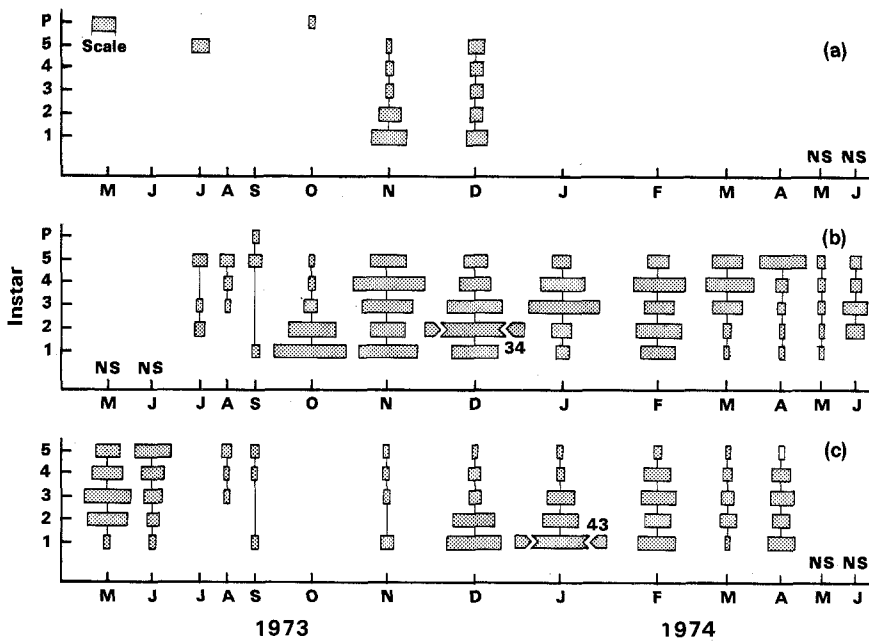


Fig. 12. Monthly instar distribution of *Aoteapsyche colonica* larvae and pupae at three Waitakere River sites. Sample sizes: site I(a) $n = 68$; site II(b) $n = 577$; site III(c) $n = 369$. Scale: 10 individuals.

Oxyethira albiceps

This hydroptilid species occurred in small numbers in both upstream sites, but was abundant at sites I and II.

For seasonal size-distribution analysis the species has been divided into the three main aquatic stages (Hickin 1967): uncased larvae (instars 1–4), cased larvae (instar 5) and pupae. If *O. albiceps* is univoltine, a sequence of larval stages from predominantly uncased larvae to cased larvae and pupae might be expected. Instead, all stages were present in most samples, although pupae were often dominant in autumn and early winter (April–July) and uncased individuals were most common during summer (Fig. 13).

Hopkins (1976) found *O. albiceps* pupae only in October and June and suggested that the species was bivoltine. Two generations per year are recorded for members of this genus in Europe (see Wiggins 1977). However, the presence of *O. albiceps* pupae throughout the year in the Waitakere system suggests that either more generations are

produced there than in the southern North Island population studied by Hopkins (1976), or that hatching and pupation were almost continuous in the Waitakere River population.

Olinga feredayi

This species of conoesucid caddis-fly was common only at the two upstream sites in the Waitakere River (see also Towns 1979).

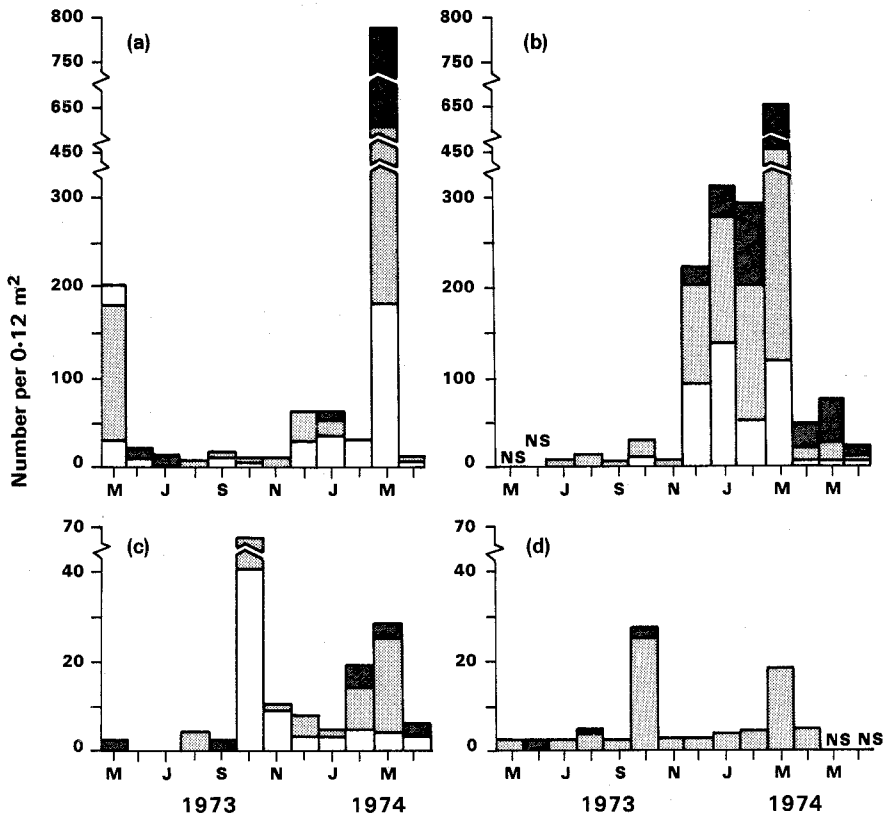


Fig. 13. Monthly changes in abundance of *Oxyethira albiceps* uncased larvae (unshaded), cased larvae (pale shading) and pupae (dark shading) at sites I(a), II(b), III(c) and IV(d) in Waitakere River. NS, no sample.

Because *O. feredayi* showed a lack of instar differentiation, larval head-capsule widths have been arbitrarily divided into five size groups (Fig. 14). The first group possibly corresponds to instar 1 of Winterbourn (1978), and mainly consisted of larvae forming cases of sand grains rather than horny material.

The life cycle of *Olinga feredayi* is difficult to interpret. There was no evidence of a larval growth pattern and group 1 individuals were present through the year, indicating an extended hatching period (Fig. 14). The species has also been studied by Hopkins (1976) in the southern North Island and by Winterbourn (1978) in the South Island. They also encountered a wide spread of size groups in any one month, although the data given by Hopkins (1976) suggest a 12-month larval life for the species.

Discussion

A few of the species discussed here have been studied elsewhere in New Zealand, although in some cases comparison with the present work has doubtful validity because of identification problems. These are a particular difficulty in the mayfly genus *Deleatidium*.

Suggested life-history strategies for species studied here are summarized in Table 2. This is based only on data from field studies, and some of the suggestions, such as delayed hatching, require confirmation by laboratory work. Despite this, the summary is well supported by those species which have been studied elsewhere in New Zealand.

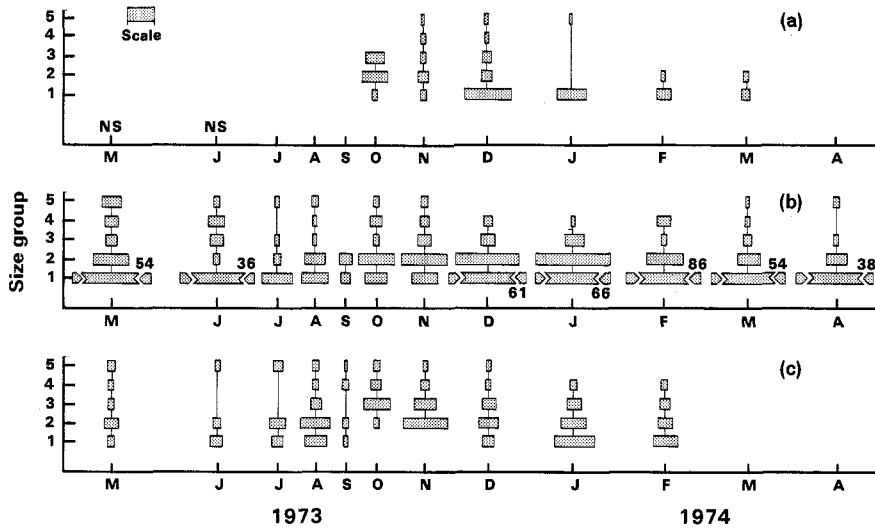


Fig. 14. Monthly size distribution of *Olinga feredayi* at sites II(a), III(b) and IV(c) in Waitakere River. Head widths of size groups: 1, 0.12–0.28 mm; 2, 0.32–0.48 mm; 3, 0.52–0.68 mm; 4, 0.72–0.88 mm; 5, 0.92–1.20 mm ($n = 1069$). Sample sizes: site II, $n = 38$; site III, $n = 744$; site IV, $n = 224$. NS, no sample.

The life cycle of *Potamopyrgus antipodarum* has been investigated in laboratory and field populations by Winterbourn (1970) in the southern North Island. Details of growth and size at maturity in the Waitakere River population closely followed Winterbourn's results. Species of *Potamopyrgus* are unusual amongst molluscs in being ovoviparous and facultatively parthenogenetic. Sex ratios of wild populations range from a predominance of females to equal proportions of each sex (Winterbourn 1973; Wallace 1978). With such reproductive flexibility release of young throughout the year is not surprising.

Most information on life cycles of lotic amphipods is based on Gammaridae, a widespread family in Northern Hemisphere streams. Gammarids are rare in New Zealand fresh waters, where eusirids predominate. The most widespread species is *Paracalliope fluviatilis* (Chapman and Lewis 1976). Some features of the reproductive biology of *P. fluviatilis* are quite distinctive. This species is much smaller than most freshwater amphipods so far studied and, possibly linked with this, the clutch size of *P. fluviatilis* (3.1) is about one-third the minimum clutch size recorded for gammarids (see Hynes 1955; Hynes and Harper 1972). Gammarids also commonly have a winter resting stage (Hynes 1955), although this does not occur in all populations of the same

species (Welton 1979). No resting stage occurred in *P. fluviatilis*, so the small clutch size was probably offset by a long reproductive season.

The leptophlebiid mayflies *Zephlebia* (*Neozephlebia*) sp. and *Deleatidium* spp. in the Waitakere River both showed a wide spread of nymphal sizes in each month and a lack of clear seasonal growth. Similar size-distribution patterns were obtained in the South Island by Winterbourn (1974, 1978) for *Deleatidium* nr *autumnale* and *D.* nr *lillii*, and by Hopkins (1976) for a southern North Island population of *D. lillii*.

The acknowledged presence of more than one species of *Deleatidium* in the present study and those of Winterbourn (1974, 1978) and Hopkins (1976) may in part explain the apparent greatly extended hatching and emergence periods found in the genus (although in each of the above studies one species apparently predominated). This raises the possibility of staggered life cycles in sympatric species of *Deleatidium*, a question investigated in an independent study (unpublished data).

Table 2. Suggested life-history strategies of common benthic invertebrates from the Waitakere River

	Strategy	Species
(1)	Facultative parthenogenesis, continuous release of young, oviviviparity	<i>Potamopyrgus antipodarum</i>
(2)	Continuous release of young, successional breeding, ovoviviparity	<i>Paracalliope fluviatilis</i>
(3)	Continuous and possibly delayed hatching, long potential emergence period	<i>Zephlebia</i> (<i>Neozephlebia</i>) sp., <i>Deleatidium</i> spp., <i>Aoteapsyche colonica</i> , <i>Oxyethira albiceps</i> , <i>Olinga feredayi</i>
(4)	Synchronized emergence, slow growth with overlapping generations	<i>Hydora nitida</i>
(5)	Rapid growth, high colonization potential, possibly multivoltine	Chironomidae, <i>Austrosimulium australense</i> , possibly <i>O. albiceps</i>

Larval Elmidae have been widely reported from New Zealand streams, but little is known of their biology. The only published study to date is for unidentified elmidae larvae by Hopkins (1976).

The data presented here support the 2-year life cycle proposed by Hopkins (1976), but the 5-month adult flight period of *Hydora nitida* in the Waitakere River (October–February) differs from the 2 months (December and February) adults of an undetermined species were observed by Hopkins (1970).

There have been few investigations of larval life histories of aquatic Diptera in New Zealand, and none on the chironomids of forest streams. Two chironomid species studied in the Waitakere River, *Austrocladius* sp. and *Paratanytarsus agameta*, were present for much of the year as pupae, suggesting that they are multivoltine. All of the dipterans predominated in the samples as late instars, including species such as *Maoridiamesa harrisi* and *Austrosimulium australense*, which were a seasonal (winter–spring) component of the fauna. Both chironomids and simuliids have a high

dispersal ability as larvae in drift (e.g. McLay 1968; Waters 1972), and this, coupled with rapid growth, would account for their lack of clearly defined life cycles.

Life-history information on more southern populations of the caddis-flies *Aoteapsyche colonica* and *Olinga feredayi* is available from the studies by Hopkins (1976) (*A. colonica* and *O. feredayi*) and Winterbourn (1978) (*O. feredayi*). Both species showed a wide spread of size classes in most months in each population, indicating prolonged hatching and emergence.

In the model presented by Hynes (1970), molluscs and Pericarida are commonly placed in the non-seasonal category because of their tendency to have overlapping generations. *Potamopyrgus antipodarum* and *Paracalliope fluviatilis* in the Waitakere River clearly fit into this group. Seasonal cycles appear to be most common amongst the insects, but none of the species in the Waitakere River have well-defined seasonal cycles (*sensu* Hynes 1970).

Recent work has provided life-cycle information for many of the more common New Zealand stream insects. In addition to the 10 species studied here, eight were studied in the southern North Island by Hopkins (1976), three taxa in lowland South Island rivers (Winterbourn 1974; Devonport and Winterbourn 1976), and nine in Middle Bush Stream, a cool stream in mountain beech forest (Winterbourn and Davis 1976; Winterbourn 1978). Although stream water temperatures in Middle Bush Stream ranged from 4.1 to 11.4 °C compared with 10.5–23 °C in the Waitakere River (Towns 1979), almost all species have non-seasonal life cycles (*sensu* Hynes 1970), with a wide spread of size classes in most months. The only exceptions are two species of gripopterygid stonefly, *Zelandobius confusus* and *Z. furcillatus*, and the oconesid caddis-fly *Zelandopsyche ingens* in Middle Bush Stream (Winterbourn 1978; Winterbourn and Davis 1976, respectively). The elmid *Hydora nitida* in the Waitakere River, for which growth is more closely synchronized, still falls into the non-seasonal category because it has overlapping generations. A few well-identified species, including *Olinga feredayi*, *Aoteapsyche colonica* and *Stenoperla prasina*, have now been studied in different parts of their geographical range. However, apart from later emergence of *S. prasina* with increased altitude (lower temperature) (Winterbourn 1978), there is little evidence so far for greater synchrony of life cycles of the same species in cool rather than warm streams.

This predominance of poorly synchronized life cycles differs from the situation commonly reported in the Northern Hemisphere, although much of the literature is based on the inhabitants of cool temperate streams, many with winter ice cover. In warmer streams, such as the Pyrenean stream studied by Thibault (1971a), life cycles of some species (of mayflies) are poorly synchronized, whereas other species have well-synchronized life cycles and a clear division of cohorts (Thibault 1971b). Similarly, some streams in northern Florida have a temperature range almost identical with that of the Waitakere River, but some seasonal mayflies are present (e.g. Pescador and Peters 1974; Tsui and Hubbard 1979).

Poorly synchronized life cycles occur also in many New Zealand terrestrial insects (cf. Roberts 1978), and Corbet (1978, p. 367) has pointed out that 'patterns of seasonality in New Zealand insects differ on the whole from those detected in the northern hemisphere . . .'. It has been suggested that poorly synchronized life cycles and a lack of diapause is a response to the mild climate of New Zealand (Devonport and Winterbourn 1976) and (for phytophagous insects) a year-round evergreen food supply (Roberts 1978). However, climate alone does not explain the differences in life-cycle patterns between warm temperate streams in the Northern Hemisphere and those

of similar streams in New Zealand. A solution may be obtained when more is known of the life cycles of insects in Southern Hemisphere temperate streams outside New Zealand. So far, the only detailed work is that of Hynes and Hynes (1975) who found a lack of seasonal rigidity in growth and emergence for Australian stoneflies, which they attributed to the effects of a harsh and unpredictable climate. This produces the curious situation in which similar patterns of seasonality in New Zealand and Australia are attributed to different climatic influences. Although the comments of Hynes and Hynes (1975) may not relate to long geological time, both Australian and New Zealand aquatic invertebrate faunas have been subjected to wide climatic variations since isolation from other southern continents (e.g. Keast 1959; Fleming 1975; Bowler 1976). These conditions, although different in the two areas, are likely to have caused selection for ecological flexibility, ultimately resulting in a predominance of non-seasonal life cycles. An alternative (or possibly additional) influence on seasonality of life cycles may be the availability of allochthonous detritus. In the Northern Hemisphere, life cycles of many stream detritivores are linked to availability of decaying leaves, i.e. autumnal leaf fall (cf. Petersen and Cummins 1974). In New Zealand and Australia litter availability ranges from seasonal with a summer peak to virtually non-seasonal (e.g. Daniel 1975; Winterbourn 1976; Lee and Correll 1978). It has been suggested that the lack of autumn leaf fall may be reflected in the life cycles of Australian stream invertebrates (Williams and Wan 1972), and this could also apply to New Zealand. However, so far the only study of seasonality of allochthonous inputs to streams is that of Winterbourn (1976) in New Zealand beech forest.

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