The macroinvertebrate fauna of a New Zealand forest stream

M. J. WINTERBOURN
Department of Zoology, University of Canterbury, Christchurch 1, New Zealand

The distribution, abundance, and life histories of benthic invertebrates were investigated in a small, *Nothofagus* forest stream in North Canterbury, South Island, New Zealand. The fauna was dominated by Trichoptera and Plecoptera; Mollusca and fish were absent. Large particle detritivores and scrapers were the predominant functional groups found. Larval Philopotamidae (Trichoptera) were the only abundant filter feeders. Nymphs of the stonefly *Spaniocerca zelandica* and of mayflies, *Deleatidium* spp., were the most abundant animals on plant detritus; *Deleatidium* spp. were abundant on stones also. The distribution of invertebrates in riffles, loose stones, pools, and plunge pools was examined using mesh colonisation trays lifted in September, November, February, and May after respectively 88, 69, 98, and 94 days *in situ*. Most species were widely distributed, and sample densities of the more abundant insect species showed weak positive correlations with the biomass of detritus present in trays in most months. The turbellarian *Neppia montana* was overrepresented in trays compared with stream samples, but the relative abundance of most other species appeared to be similar to that on the stream bed. A large amount of silt accumulated in trays during a heavy flood, and was colonised mainly by the oligochaete *Eiseniella tetraedra*. Information on the life histories of 15 species of Plecoptera, Trichoptera, Ephemeroptera, and Coleoptera was obtained from a 1-year monthly sampling programme, in which 36 taxa were distinguished, and from collections of adult insects made over a 3–4-year period. Most species had poorly synchronised life histories, in that a wide size range was apparent among individuals in most months. Eight species emerged in at least 4 months; *S. zelandica* and the philopotamid *Hydrobiosella stenocerca* were taken in 8 and 9 months respectively.

INTRODUCTION

The benthic invertebrate communities of rivers and streams in New Zealand have received limited attention from biologists. Lists of macroinvertebrate species and some quantitative data have been given by several workers following short-term benthic surveys—see references in Bayly & Williams (1973)—and in papers concerned primarily with invertebrate drift (McLay 1968, Cadwallader 1975, Fowles 1975) and insect feeding and life histories (Crosby 1975, references in Devonport & Winterbourn 1976). The most important published studies on the communities of streams in New Zealand, by Allen (1951) and Hopkins (1970), are concerned primarily with the benthos as a source of food for trout and other fish. They provide some information on seasonal changes in numbers and biomass of invertebrates, and Allen (1951) discusses the life histories of some species. The thesis by Towns (1976) on the benthic communities of a kauri forest stream in the Waitakere Ranges near Auckland is the most comprehensive study of a stream fauna made to date, and provides details of the life histories, population changes, and distribution of a large number of taxa.

This paper presents the results of a study of the benthic fauna of a small stream which flows through a stand of mountain beech forest in the South Island of New Zealand. The life histories and seasonal changes in abundance of the more plentiful insect species were examined, and the distribution of invertebrates in different biotopes was investigated using colonisation trays.

STUDY AREA

Middle Bush Stream is located at Cass on the eastern slopes of the Southern Alps (43°02′S,171°46′E). It arises from a constant-temperature spring (6–7°C) 850 m above sea level; at about 700 m a.s.l. it enters a 3–4-ha stand of mountain beech (*Nothofagus solandri* var. *cliffortioides*). Soon after leaving the forest it disappears underground, except for short periods when swollen by heavy or continuous rainfall. A detailed description of the stream and its catchment is given by Winterbourn & Davis (1976).

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The work described here was carried out in the forested section of the stream, which has an average gradient of 1 in 3, steep banks, and a boulder-strewn bed less than 2 m wide. Mosses grow on some rock faces, and logs and branches are scattered over the bed. Beech litter enters the stream throughout the year, and leaves and twigs become trapped among stones and branches. At times large piles of trapped debris project out of the water or accumulate on the bed of pools (Winterbourn 1976).

Stream discharge measured semi-continuously at a weir 93 m below the upper tree line from September 1973 to March 1975 averaged 5 litres/s. Water temperature during the same period ranged from 4.1°c to 11.4°c (Winterbourn 1976).

METHODS

Macroinvertebrates inhabiting plant detritus (mainly dead leaves and twigs) and stony substrates were sampled at approximately monthly intervals from April 1973 to March 1974. On each occasion six collections of detritus, each of about 100 g dry weight, were made by enclosing material in a 0.2-mm-mesh net. Most detritus was collected from pools, where it occurred in discrete piles. However, after periods of high discharge the amount of detritus in pools was reduced, and some collections were made among large stones where plant debris, particularly sticks, had been trapped. Each month two collections were made from stony substrates at sites where only small amounts of plant detritus appeared to be present. They were taken by disturbing the substrate with the feet and brushing the surfaces of stones so that all material was washed into a net. All samples were preserved immediately with formalin, and later sorted in white trays after fine silt and mud had been removed by washing through a 0.2-mm-mesh sieve.

Table 1. Macroinvertebrates taken in samples of detritus and stones, Middle Bush Stream, April 1973–March 1974. Percentage composition values are means of all monthly percentages (+, >0.5% of the total fauna; *, not considered in this study; —, not present)

	Composition (%)	
	Detritus	Stones
EPHEMEROPTERA		
Siphlonuridae		
Nesameletus sp.	+	7.5
Leptophlebiidae		
Deleatidium spp.	17.3	57.2
PLECOPTERA		
Eustheniidae		
Stenoperla prasina (Newman)	+	0.9
Austroperlidae		
Austroperla cyrene (Newman)	4.2	1.1
Gripopterygidae		
Zelandobius furcillatus Tillyard	+	3.1
Zelandobius confusus (Hare)	7.7	5.3
Acroperla spiniger (Tillyard)	+	+
Zelandoperla fenestrata Tillyard	+	+
Notonemouridae		
Spaniocerca zelandica Tillyard	30.1	5.1
Cristaperla fimbria (Winterbourn)	–	+
TRICHOPTERA		
Oeconesidae		
Zelandopsyche ingens Tillyard	8.7	+
Philorheithridae		
Philorheithrus agilis (Hudson)	2.6	0.6
Philopotamidae		
Hydrobiosella stenocerca Tillyard	+	4.1
Leptoceridae		
Hudsonema aliena (McLachlan)	+	+
Sericostomatidae		
Olinga feredayi (McLachlan)	2.7	2.8
Rhyacophilidae		
Edpercivalia maxima (McFarlane)	0.5	+
Hydrobiosis spatulata McFarlane	+	+
Costachorema psaroptera McFarlane	+	0.8
Hydrochorema crassicaudatum Tillyard	+	+
MECOPTERA		
Nannochoristidae		
Microchorista philpotti (Tillyard)	+	+
COLEOPTERA		
Helodidae		
Species A	12.4	1.7
Species B	+	+
Hydraenidae		
Indet.	0.9	3.4
Hydrophilidae		
Indet.	+	+
Staphylinidae		
Indet.	+	+
Elminthidae		
Indet.	+	+
DIPTERA		
Tipulidae		
Hexatomini	0.6	1.0
Muscidae		
Limnophora sp.	+	+
Dixidae		
Paradixa sp.	+	+
Simuliidae		
Austrosimulium ungulatum Tonnoir	+	+
Empididae		
Indet.	+	+
Ceratopogonidae		
Indet.	+	—
Chironomidae		
Tanytarsini, Tanypodinae	*	*
TURBELLARIA		
Planariidae		
Neppia montana (Nurse)	—	+
OLIGOCHAETA		
Lumbricidae		
Eiseniella tetraedra (Savigny)	2.7	1.3
NEMATOMORPHA		
Gordiidae		
Gordius sp.	+	+

Adult insects and final nymphal exuviae were collected by beating stream-side vegetation with a net and by systematically turning over stones and logs on and beside the stream bed. Many exuviae as well as adult Plecoptera and Trichoptera were taken from the faces of the weir. Pupae and egg masses were collected from various substrates within the stream. Searches for adult insects, eggs, and pupae were continued after March 1974 to provide further information on the life histories of some species.

Head capsule widths of nymphs and larvae of some of the more abundant insects were measured with a linear eyepiece graticule at $\times 25$ for use in determining life histories. Usually all individuals collected each month were measured, but sometimes subsamples of 50–70 nymphs of *Deleatidium* spp., *Spaniocerca zelandica*, and *Zelandobius confusus*, taken as described by Winterbourn (1974), were measured.

To investigate the distribution and abundance of benthic invertebrates, 20 square, nylon-mesh trays (1.0-mm mesh; area 0.06 m^2; height of sides 40 mm) were placed on or embedded in the stream bed on four occasions between June 1974 and May 1975 and left for 2–3 months. Trays contained stones and gravel, several loosely packed stones, or one large stone (see Winterbourn 1976), and were arranged so as to sample the main biotopes (Macan 1963, p.8) in proportion to their abundance. After collection, the contents of trays were sorted into animals, inorganic sediments, coarse detritus (mainly leaves and twigs), and fine detritus (material passing through a 2.0-mm-mesh sieve). All animals were identified and counted; other components were dried and weighed.

THE FAUNA

Thirty-six taxa were distinguished in the monthly sampling programme (Table 1). The fauna was dominated by nymphal and larval insects; Trichoptera (9 species) and Plecoptera (8 species) were best represented. No molluscs or fish were found. The Chironomidae present—predominantly small species of Tanytarsini and Tanypodinae—were not considered in the study, although their larvae are sometimes abundant on decaying beech leaves (Davis & Winterbourn 1977).

The composition of the faunas inhabiting detritus and stony substrates differed in several respects. *Spaniocerca zelandica* was the most abundant animal on detritus in most months, and *Deleatidium* spp. were also common. Larvae of an helodid beetle were important, especially in late winter and spring, whereas *Zelandobius confusus* was common in summer. The large larvae and nymphs of *Zelandopsyche ingens* and *Austroperla cyrene* were conspicuous members of the detritus fauna but were found infrequently on stones.

On stony substrates, nymphs of *Deleatidium* spp. were the most abundant animals throughout the year; nymphs of a second mayfly, *Nesameletus* sp., were also common. The most abundant caddis was the retreat-dwelling philopotamid *Hydrobiosella stenocerca*. *Spaniocerca zelandica* made up only 2–12% of the fauna each month, but two species of *Zelandobius* were abundant in summer.

IDENTITY OF 'DIFFICULT' SPECIES

In most instances, nymphal and larval stages of the more common species were associated with their adult stages by rearing. However, this did not always permit positive identification of the species, since available descriptions of many adult insects are inadequate and give little or no indication of intraspecific variability. The identities of 'difficult' species encountered in this study are discussed below.

TRICHOPTERA. Although apparently only one species of *Olinga* occurred in Middle Bush Stream, its identity was difficult to establish. *O. jeanae* McFarlane has been recorded by Cowley (1975) from Middle Bush, and its type locality—Reservoir Bush, Cass—is only about 200 m away. According to McFarlane (1966), *O. jeanae* differs from the more common *O. feredayi* mainly in colour and size. Adult females reared from Middle Bush larvae were intermediate in size between published figures for the two species, and were variable in colour. Larvae possessed some features in common with each species as described and figured by Cowley (1975), and were identical to larvae from a number of other localities in Canterbury. They were considered to be *O. feredayi* by McFarlane (pers. comm.), and this name is used here.

In his recent faunal study, Neboiss (1977) refers all Australasian Philopotamidae formerly in *Dolophilodes* to *Hydrobiosella*. Larvae of *H. stenocerca* were identified from Cowley's (1975) description, and all adults taken fitted his amended description of that species (Cowley 1976).

EPHEMEROPTERA. Species of *Deleatidium* and *Nesameletus* cannot be determined from the descriptions in Phillips (1930), the most recent revision of the New Zealand Ephemeroptera. Abdominal pigmentation and gill morphology suggested that most *Deleatidium* nymphs taken in the forested section of the stream belong to a single species. Since their gills had pointed tips they could be assigned to the informal *lillii* species-group (R. M. Ogilvie & D. R. Towns, pers. comm.). Nymphs belonging to the *myzobranchia* species-group—which is characterised by rounded gills—also occurred, but were most common outside the forest.

PLECOPTERA. The two *Zelandobius* species were difficult to identify with certainty even though the genus has been revised by McLellan (1969). Adults of the larger species resembled those of the variable *Z. confusus*. However, nymphs differed from 'typical' *confusus* in having the pronotum slightly more rectangular and the vestiture of hairs on the abdomen reduced to narrow, transverse and longitudinal median bands on each tergite. I have seen nymphs from elsewhere intermediate between the Cass and the 'normal' *confusus* condition, so it seems reasonable to include the Middle Bush population in *Z. confusus*.

The smaller species is almost certainly *Z. furcillatus*. Adults fit McLellan's (1969) description well, and possess the patch of short, dark hairs on tergite 10 which helps distinguish this species from *Z. unicolor* Tillyard. However, nymphs are somewhat intermediate between *unicolor* and *furcillatus* as described by McLellan (1969); the pronotum is intermediate in shape, and the abdominal tergites are ridged in the midline, this ridging being particularly pronounced in small individuals.

LIFE HISTORIES OF SELECTED SPECIES

In this section, discussion of the larval or nymphal stage of the life history is based on the monthly sampling programme (April 1973–March 1974) unless otherwise stated, whereas information on the duration of the egg, pupal, and adult stages was accumulated over several years.

PLECOPTERA

Spaniocerca zelandica

Nymphs in a wide range of size classes occurred in all months, and the final instar was found in every month except May. Fig. 1 indicates that the major component of the population was increasing slowly in body size from April, when the study began, to November, when the number of late-instar nymphs present decreased. Small nymphs predominated in December, and the modal size group subsequently increased in body size until March. This suggests that *S. zelandica* is univoltine. Adults were taken from September to April and in July; maximum numbers were present in October and November. Numbers of nymphs per 500 g dry weight of detritus ranged from 70 in November, the time of peak emergence, to 540 the following February (Fig. 2).

Austroperla cyrene

Nymphs of most sizes were present in all months; the final instar occurred from April to October (see Fig. 1). Their densities in samples ranged from 10 to 50 nymphs per 500 g detritus, with maximum numbers in summer (Fig. 2). Development times could not be estimated from monthly size frequency data, and it is unclear whether the life history is univoltine or more protracted. Hynes & Hynes (1975) concluded that the Australian Austroperlidae grow very slowly, even the smallest species—*Acruroperla atra* (Samal)—taking 3 years to complete development. *A. cyrene* adults were taken from September to January, and maximum emergence apparently occurred in early summer.

Zelandobius confusus

The annual cycle of *Z. confusus* is apparent from the field data (see Fig. 1). Very small nymphs first appeared in October, and growth continued throughout the summer; many individuals apparently overwintered in the final instar. Few large individuals were taken in monthly samples (Fig. 2), but fieldwork carried out in the winter and spring of 1976 showed that final-instar nymphs inhabited partly emergent logs and stones and were active (though sluggish) at temperatures as low as 3°C. Recently emerged adults were taken from stones immediately above the water and beaten from streamside vegetation in September 1976; none were seen in other months. The presence of very small nymphs in litter bags removed from the stream in September (Winterbourn, in press) suggests that eggs have a short incubation period.

Zelandobius furcillatus

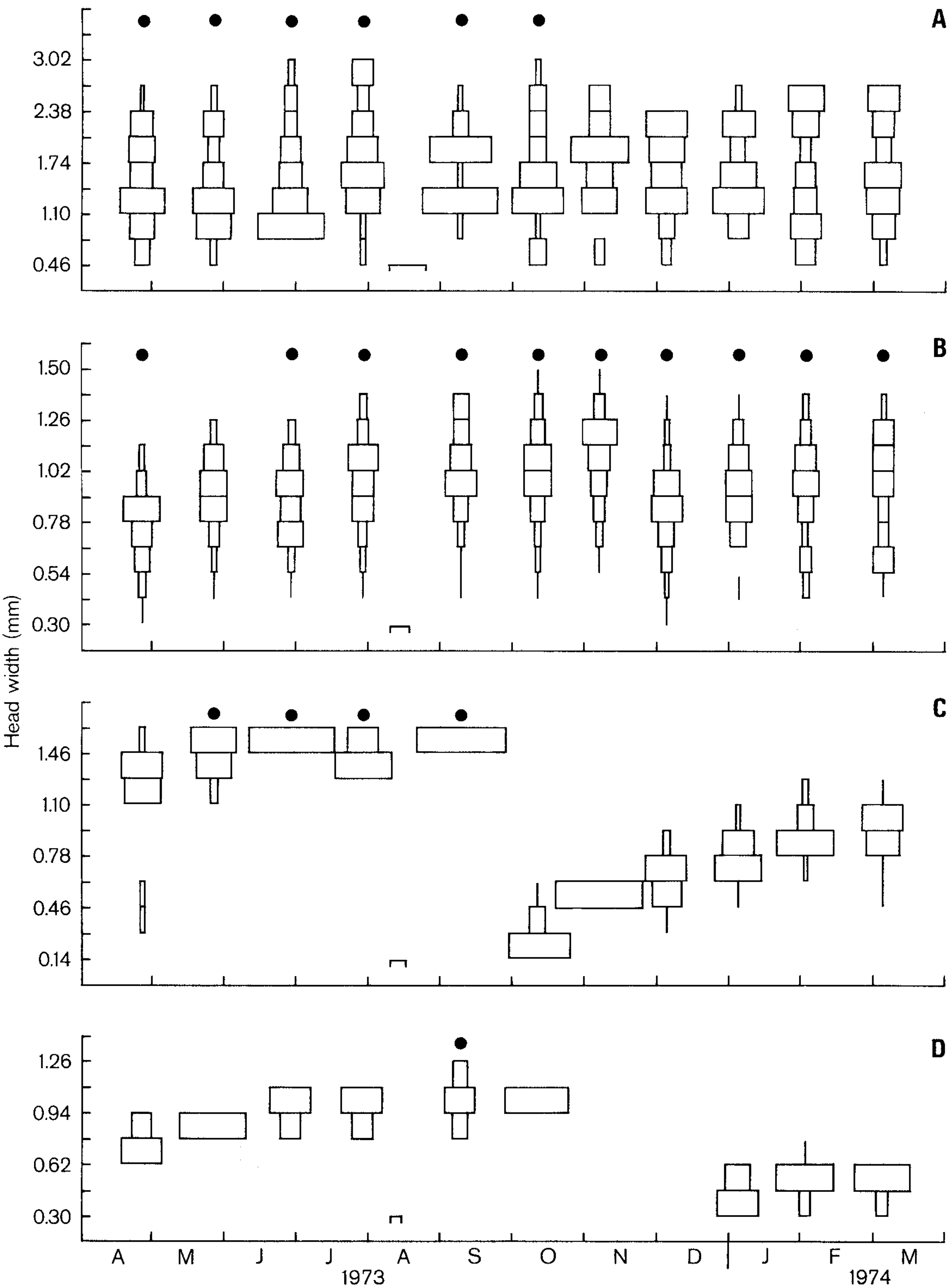
This species was less common than *Z. confusus*, and only small numbers of nymphs occurred in monthly samples; however, its life history could be followed. Small nymphs were seen in January, when no large individuals were taken. Increasingly large nymphs were found in autumn and winter, and the final instar appeared in September (see Fig. 1). Adults were collected in September, November, and December.

OTHER PLECOPTERA

Nymphs of the large, carnivorous eustheniid *Stenoperla prasina* were found in most months. However, they were too few for any conclusions to be drawn regarding growth or the duration of nymphal life. Small individuals and final-instar nymphs were taken in December–February, whereas final exuviae or adults were collected in February–April and June.

(Opposite page)

Fig. 1. Distribution of nymphal size classes of stoneflies *Austroperla cyrene* (A), *Spaniocerca zelandica* (B), *Zelandobius confusus* (C), and *Z. furcillatus* (D), Middle Bush Stream (●, final-instar nymphs present). Scale line: 20% of the individuals in each monthly sample.


A
3.02
2.38
1.74
1.10
0.46
B
1.50
1.26
1.02
0.78
0.54
0.30
Head width (mm)
C
1.46
1.10
0.78
0.46
0.14
D
1.26
0.94
0.62
0.30
A
M
J
J
A
S
O
N
D
J
F
M
1973
1974

Nymphs of *Acroperla spiniger* were taken sporadically. Small individuals occurred in samples of stones and detritus from the stream, but large nymphs are semiterrestrial, and were taken among stones at the stream margin. During the day they remained beneath the stones, but at night many were seen crawling over them and feeding on mosses and other crustose plants. Large nymphs were plentiful in this habitat in October and November, the only months in which adults were found.

Two other stonefly species were found in the forested section of Middle Bush Stream. *Zelandoperla fenestrata* was uncommon there, but its nymphs were abundant on rock faces and mosses near the source of the stream. Numerous adults of *Cristaperla fimbria* were collected beside the stream from October to January, but only two nymphs were found in monthly samples; the main nymphal habitat was not discovered. Observations made in other forest streams suggest that most nymphs live in muddy-bottomed pools or backwaters, but such habitats are uncommon in Middle Bush Stream.

TRICHOPTERA

Philorheithrus agilis

Egg masses were found attached to the undersides of stones and logs in running water in December–February. They were spherical, 4.5–8.0 mm in diameter, composed of soft, colourless jelly coated with fine detrital particles, and contained several hundred eggs each 0.30–0.34 mm in diameter.

Five larval instars could be distinguished on the basis of head-capsule width. First-instar larvae were collected from the stream and hatched from eggs in the laboratory, but none occurred in the monthly samples. It is likely that many larvae grow rapidly and reach instar 4 or 5 during autumn, but growth appears not to be closely synchronised throughout the population (Fig. 3). Sampled densities ranged from 0 to 41 per 500 g of detritus (see Fig. 2), the final instar predominating in all months except March.

Pupae were found attached to stones in late spring and summer, but no adults were seen.

Zelandopsyche ingens

The larval and pupal stages of *Z. ingens* in Middle Bush Stream have been discussed by Winterbourn & Davis (1976). Since then the egg has been discovered, and more is known about the flight period of the adult. Briefly, most young larvae appear in winter and spring and the final instar is attained in summer or early autumn. Most individuals overwinter in the final instar, and pupae have been found in January and February. *Z. ingens* is the largest and most abundant caddisfly inhabiting piles of detritus in the stream; sampled densities ranged from 25 to 126 larvae per 500 g of detritus (see Fig. 2).

A single egg mass was found in July 1976 attached to a log in still water at the side of the stream near the lower tree line. Some eggs were hatching and some larvae had already left the egg mass. The water temperature was 3°C. The egg mass resembled that of *Philorheithrus agilis*, but was larger (12–13 mm in diameter), as were the eggs (0.7 mm in diameter). Newly hatched larvae had head widths of 0.48 mm, which confirms that instar F-4 of Winterbourn & Davis (1976) is instar 1.

Recently emerged adults were collected from Middle Bush Stream and the adjacent Reservoir Bush Stream on 3 and 17 April 1976, and 15 spent individuals (9 males, 6 females) were taken at the edge of the Hawdon River, about 5 km north of Cass, on the latter date. These records extend the known flight period of this species, which has been seen as early as January (Winterbourn & Davis 1976). The discovery of an egg mass in July indicates that some individuals are active after April, and because first-instar larvae can be found in spring it seems likely that some adults overwinter.

Olinga feredayi

Free, spherical egg masses 2.8 mm in diameter were found in February and November 1974 and February 1975; they resembled those described by Pendergrast & Cowley (1966).

With the exception of the first instar, which had a head width of 0.15 mm and was obtained from eggs hatched in the laboratory, larval instars could not be distinguished on the basis of head measurements. Therefore, larvae other than first instars were placed in four size classes delimited on the assumption that there are five instars. No first-instar larvae occurred in monthly samples, but larvae belonging to the three largest classes occurred in all months (Fig. 3). Sampled densities ranged from 7 to 38 larvae per 500 g of detritus, and were highest in late summer (see Fig. 2).

Pupae were found from October to January attached to the undersides of stones and logs, but no adults were seen in the field.

Hydrobiosella stenocerca

Adults of *H. stenocerca* were the most frequently collected caddisflies around Middle Bush Stream; their flight period extended from September to May. Larvae occupied stocking-like tubes attached to the lower surface of stones in flowing water. They were taken in small numbers in most months. Late instars were most abundant in November–January.

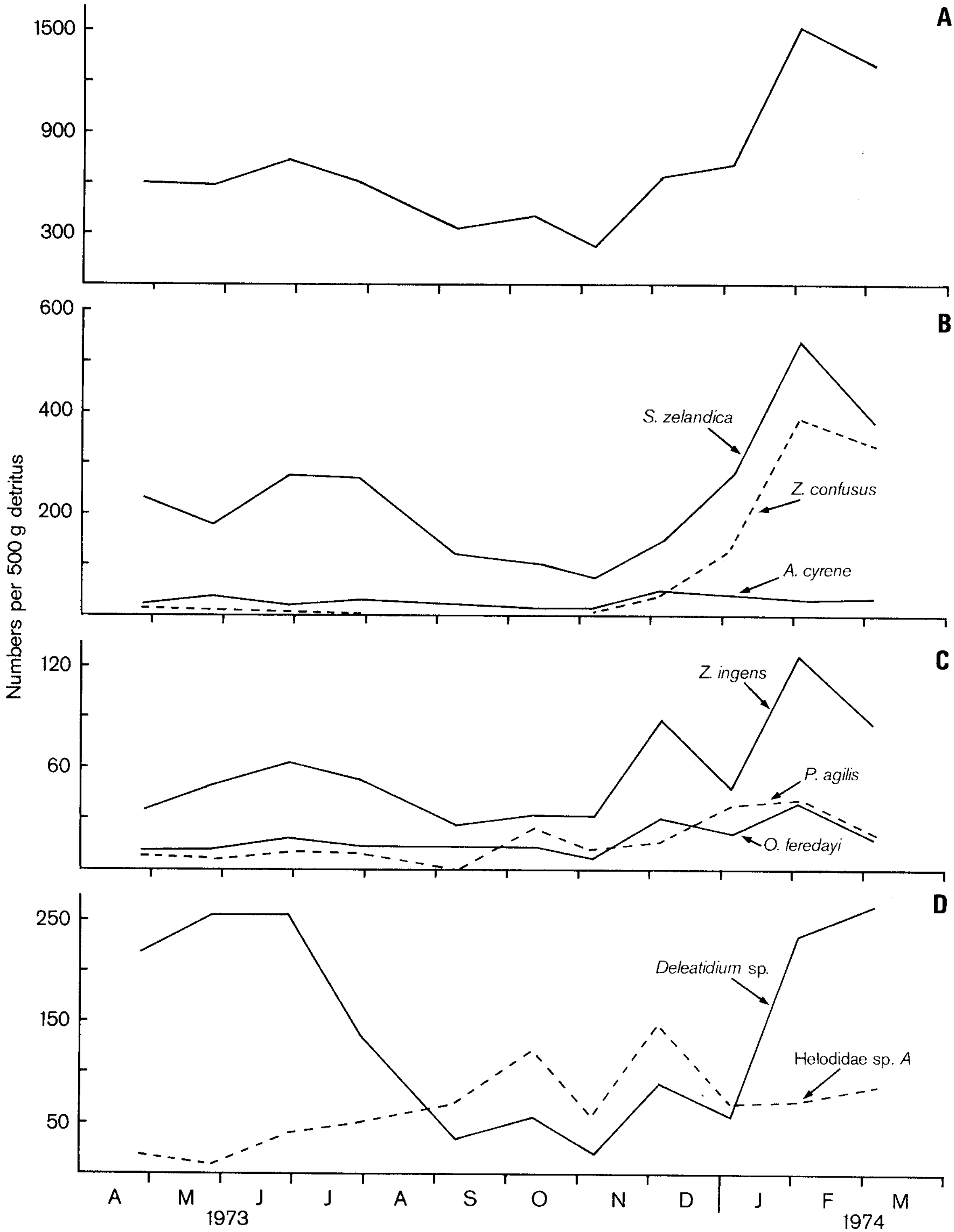


Fig. 2. Mean densities of invertebrates in monthly detritus samples, Middle Bush Stream (A, total invertebrates; B, Plecoptera; C, Trichoptera; D, Ephemeroptera and Coleoptera).

EPHEMEROPTERA

Deleatidium spp.

Nymphs of *Deleatidium* spp. were the most abundant animals taken in samples of stones, and were numerous on detritus also. The size distribution of the nymphal population each month is shown in Fig. 3, where data for animals from either substrate are displayed separately. Individuals of various sizes were present on both substrates in each month, but the proportions of nymphs in different size classes was not the same. At all times a greater proportion of small nymphs occurred on detritus, whereas larger nymphs predominated on stones. Final-instar nymphs were present from November to March.

Numbers of nymphs in detritus samples varied seasonally, with a maximum in summer–autumn and a minimum in spring (see Fig. 2). The winter decline does not necessarily indicate a reduction in population size, since many of the larger individuals may have been occupying stones at that time. The rapid increase in numbers of animals present in detritus samples in February mainly reflects the appearance of small nymphs of a new generation.

Nesameletus sp.

This was the only other mayfly inhabiting the forested section of the stream. Its nymphs rarely occurred in detritus samples but were fairly common among stones. As for *Deleatidium* spp., a range of different-sized nymphs occurred throughout the year. Winged stages were taken from November to March.

COLEOPTERA

HELODIDAE

Larvae of two species of Helodidae were taken, but could not be identified further because their non-aquatic pupal and adult stages are unknown. The only larval helodid described from New Zealand belongs to "Helodid genus D" (Bertrand 1969).

Larvae of my Species A were important members of the fauna inhabiting detritus, and occurred at densities of 10–120 per 500 g (see Fig. 2). They are large particle detritivores which feed by rasping away the tissues of dead beech leaves (Davis & Winterbourn 1977).

The number of larval instars possessed by helodids is not known, but may be large, at least in some species (Kraatz 1918). The instars of Species A could not be distinguished from head measurements, so the larval stage was divided into six equal size classes in order to investigate seasonal changes in population structure. The histograms in Fig. 3 are rather difficult to interpret, but suggest that the species may be univoltine, growth occurring principally in spring and summer and many larvae overwintering as small individuals. Alternatively there may be an additional, fast-growing winter generation, but this seems less likely.

COLONISATION TRAY STUDIES

Trays were collected in September and November 1974 and February and May 1975 after they had been in the stream for 88, 69, 98, and 94 days respectively. During these periods detritus and additional sediment accumulated in the trays, and they were colonised by invertebrates. No significant difference ($P>0.05$) was found between the mean amounts of coarse detritus (mainly leaves and sticks) and fine detritus (material passing through a 2-mm-mesh sieve) occurring in trays placed in different biotopes, and considerable variation was found between trays within groups (Winterbourn 1976). Mean dry weights of coarse/fine detritus present in September, November, and February were 18.8/4.6 g, 12.7/4.8 g, and 34.4/12.7 g per tray respectively [not g/m^2 as shown in Winterbourn (1976), fig. 7]. Only six trays were recovered in May because heavy flooding damaged or washed away the remainder. They were filled with silt and gravel, but still contained an average of 17.2 g coarse and 7.8 g fine detritus.

Mean numbers of macroinvertebrates present in the trays in the first 3 months are shown in Table 2. Twenty-seven taxa (excluding Chironomidae) were found; *Neppia montana*, *Deleatidium* spp., and *Spaniocerca zelandica* were numerically dominant. *Eiseniella tetraedra* was the dominant species in May (Table 3), when the large amounts of fine sediment present probably made conditions particularly suitable for it. In contrast, the conditions appeared to be unfavourable for *N. montana*.

Faunal density was greatest in September but only a little lower in the other months (Table 4). Numbers of some taxa—e.g., *Deleatidium* spp. and *Spaniocerca zelandica*—declined during the study period, and this may be associated with their main periods of adult emergence in spring and summer. In contrast, numbers of *Eiseniella tetraedra* increased with the advent of summer as new individuals hatched from cocoons, which were abundant in February and May (Table 4).

Total numbers of animals and numbers of the five most abundant insect species—*Deleatidium* spp., *Spaniocerca zelandica*, *Olinga feredayi*, *Zelandopsyche ingens*, and Helodidae Species A—occurring in the pool, riffle, and loose stones biotopes each month (except May) were compared using the non-parametric Kruskal-Wallis test (Elliott 1971). Plunge pools were omitted from the comparison because of the small number of sampling units used. The only significant differences ($P<0.05$) between biotopes were for *Deleatidium* spp. in September and for the total fauna, *Deleatidium* spp., *Z. ingens*, *O. feredayi*,

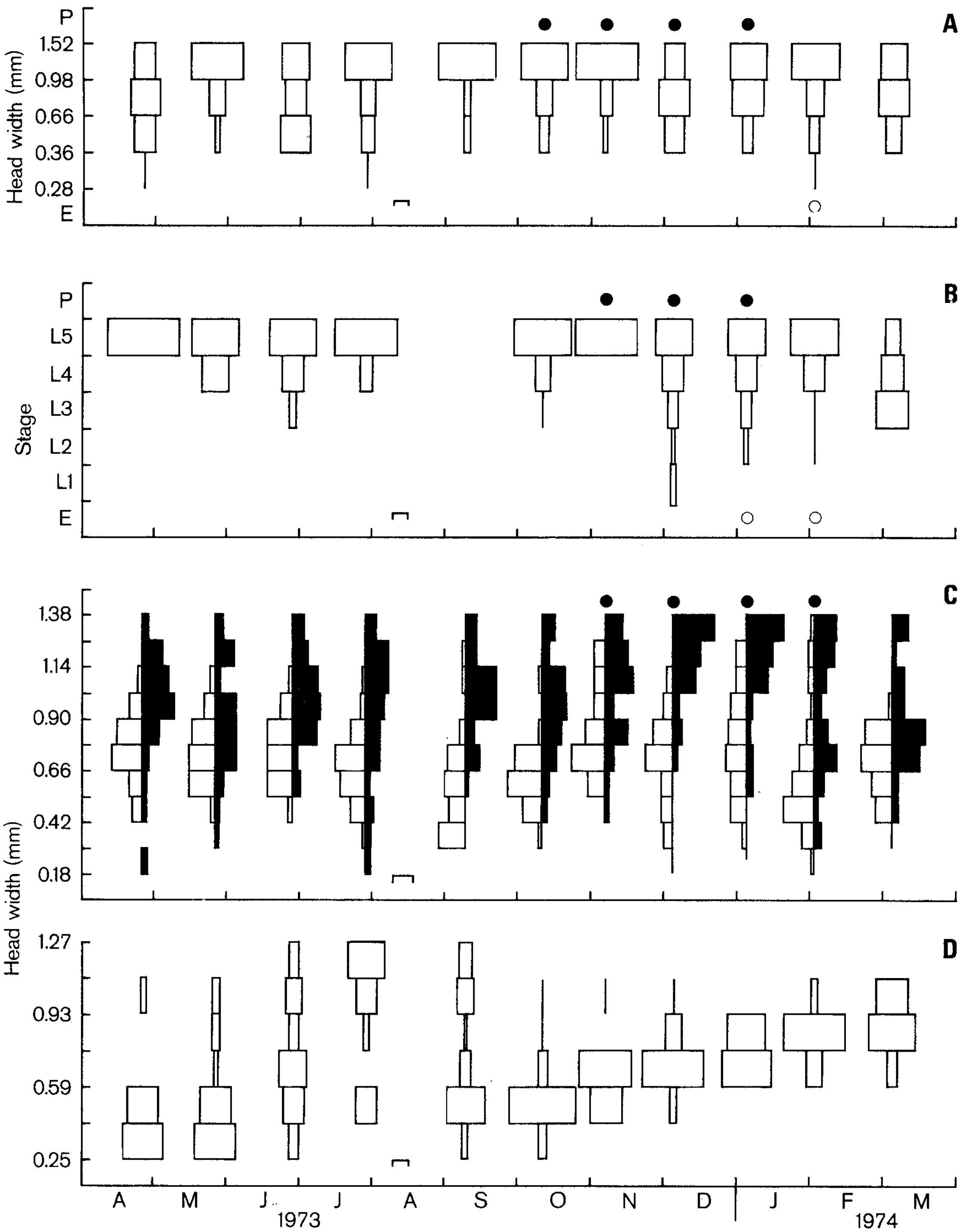


Fig. 3. Distribution of larval and nymphal size classes of the caddisflies *Olinga feredayi* (A) and *Philorheithrus agilis* (B), the mayfly *Deleatidium* (C), and the beetle Helodidae Species *A* (D), Middle Bush Stream. The *Deleatidium* histograms show nymphs from stones (shaded) and from detritus (unshaded). Conventions as for Fig. 1, plus: E. ○, eggs present; P, pupae present.

and Helodidae Species A in February. Mann-Whitney U-tests made between pairs of biotopes for these taxa gave the following significant differences at the 5% level:

September – *Deleatidium* spp. in riffles > pools

February – Total fauna in riffles and loose stones > pools

Deleatidium spp. in loose stones > pools

Olinga feredayi in riffles > pools

Helodid Sp. A in loose stones > pools and riffles

Zelandopsyche ingens in pools > riffles

Table 2. Mean numbers of invertebrates present in colonisation trays placed in 4 stream biotopes for 2–3 months and removed in September 1974, November 1974, and February 1975 (R, riffle; S, loose stones; P, pool; PP, plunge pool; —, nil)

Month removed	September				November				February			
Period *in situ* (d)	88				69				98			
Biotopes	R	S	P	PP	R	S	P	PP	R	S	P	PP
No. of trays	6	4	7	3	6	4	7	3	6	4	7	3
Nesameletus sp.	2.2	1.7	1.4	1.0	7.3	4.0	3.7	6.0	2.7	1.5	1.7	3.3
Deleatidium spp.	27.8	12.0	12.0	7.3	17.7	11.5	7.6	5.7	13.3	16.2	4.9	4.3
Stenoperla prasina	1.0	0.5	—	—	1.2	0.5	—	—	2.8	0.2	0.6	—
Austroperla cyrene	4.2	3.5	0.3	—	2.2	4.0	—	1.7	2.7	5.7	1.0	3.3
Zelandobius confusus	0.3	0.7	0.9	0.7	0.2	0.2	—	—	0.2	1.5	1.1	2.7
Acroperla spiniger	0.2	—	—	—	—	—	—	—	—	—	—	—
Zelandoperla fenestrata	—	—	—	—	—	0.2	—	—	—	—	—	—
Spaniocerca zelandica	13.5	5.7	8.6	14.3	8.8	7.7	8.3	4.3	3.3	6.7	6.0	4.3
Cristaperla fimbria	—	—	—	—	—	—	0.1	—	—	—	—	—
Zelandopsyche ingens	2.2	7.5	8.7	5.7	3.3	3.7	5.1	1.7	1.8	4.2	6.9	5.0
Philorheithrus agilis	6.0	5.7	7.1	4.7	5.3	3.7	3.9	2.0	2.8	8.5	7.4	3.7
Hydrobiosella stenocerca	4.3	1.2	—	0.7	2.0	3.5	—	0.3	2.0	10.2	0.4	0.7
Olinga feredayi	4.5	5.5	2.1	0.7	4.8	5.2	1.1	1.0	10.8	6.5	3.0	2.0
Hydrochorema crassicaudatum	—	—	—	—	0.7	2.0	0.3	—	—	—	0.1	—
Microchorista philpotti	0.2	0.2	—	—	—	0.2	—	—	—	0.2	—	0.3
Helodidae Species A	0.8	13.0	5.6	1.3	3.3	4.2	2.6	0.7	0.7	10.0	1.0	6.3
Helodidae Species B	—	—	—	—	—	—	0.1	—	0.3	1.2	0.1	—
Hydraenidae	0.7	1.0	—	—	0.2	0.7	0.3	—	0.5	0.2	—	—
Hydrophilidae	—	—	—	—	—	0.2	—	—	—	—	—	—
Elminthidae	1.0	0.2	0.3	—	—	—	—	—	—	—	—	—
Tipulidae	0.3	—	—	—	0.8	0.2	—	0.3	3.0	1.2	—	—
Limnophora sp.	0.3	—	—	—	—	—	—	—	—	—	—	0.3
Austrosimulium ungulatum	0.2	0.2	—	—	—	0.2	—	—	—	0.2	—	0.3
Neppia montana	12.0	30.0	21.0	24.7	21.2	26.2	16.1	6.0	10.8	18.5	5.9	6.7
Eiseniella tetraedra	0.2	0.7	0.1	0.7	4.8	1.5	2.4	1.3	21.0	10.0	3.9	0.3
E. tetraedra cocoons	0.8	1.7	—	—	2.8	3.2	1.6	0.7	25.7	7.0	1.9	—
Other Oligochaeta	—	—	—	—	—	—	—	—	—	0.7	0.6	0.3
Mean no. per tray*	82.7	91.0	68.1	61.8	86.8	82.8	53.2	31.7	104.4	110.4	48.6	43.8
No. of species†	20	16	13	11	17	19	15	12	17	18	18	15

*Excludes *E. tetraedra* cocoons and Chironomidae

†*Deleatidium* and the Hydraenidae are considered as single species

Table 3. Composition (%) of the fauna recovered from 6 colonisation trays, May 1975; all trays had been filled with gravel, silt, and plant debris by floodwater

Eiseniella tetraedra	49.5
Deleatidium spp.	12.8
Olinga feredayi	6.5
Philorheithrus agilis	5.2
Neppia montana	3.9
Hydrobiosella stenocerca	3.4
Austroperla cyrene	3.1
Helodidae Species A	2.9
Others	12.7
Total animals collected	382
No. of species taken	19

Table 4. Densities (no./m²) of the more abundant invertebrate species recorded in colonisation trays in 4 months

	Sept.	Nov.	Feb.	May
Total fauna	1242	1026	1082	1019
Nesameletus sp.	26	81	35	11
Deleatidium spp.	257	178	154	131
Austroperla cyrene	33	27	45	32
Spaniocerca zelandica	166	124	82	19
Zelandopsyche ingens	97	61	73	13
Philorheithrus agilis	98	64	91	53
Hydrobiosella stenocerca	26	22	46	35
Olinga feredayi	53	49	94	67
Helodidae Species A	96	46	56	29
Neppia montana	330	290	160	40
Eiseniella tetraedra	13	45	155	504
E. tetraedra cocoons	10	34	156	163

Overall, marked differences between biotopes were not evident, and considerable variation in numbers of each taxon was found between trays within each biotope. In February, when all but one of the statistically significant differences were found, discharge was very low (Winterbourn 1976) and movement of water through pools was very slow. The dissolved oxygen concentration of the water within piles of detritus lying in pools was perhaps lowered at that time, producing conditions suboptimal for respiration and therefore for colonisation by some species.

The relationship between animal numbers and dry weight of coarse and fine detritus in trays was examined for all months except May by calculating Spearman's rank correlation coefficient, r_s (Elliott 1971). The same taxa were considered as in the biotope comparison above. Positive correlations were obtained between both grades of detritus and all taxa except *Zelandopsyche ingens*, which was negatively correlated with fine detritus in February, and *Olinga feredayi*, which showed no correlation in September. Most correlations were weak, however; the few which were significant are shown in Table 5. Although a significant correlation was found between the total fauna and coarse and fine detritus in all months, no individual species showed such a consistent association, and only *Spaniocerca zelandica* was correlated significantly with either type of detritus (fine) in each month. The four species which showed one or more strong correlations with coarse detritus biomass are known to feed on dead leaves (Davis & Winterbourn 1977), whereas *S. zelandica* and *Deleatidium* spp. also ingest small detrital particles, which may help explain their association with fine detritus.

DISCUSSION

The predominant functional groups of macroinvertebrates in the forested section of Middle Bush Stream were large particle detritivores and scrapers (Cummins 1973). They feed by ingesting pieces of leaf and other dead plant material and by scraping the surface of stones and plant debris. With the exception of a few simuliid larvae and the caddisfly *Hydrobiosella stenocerca* filter-feeding species were absent, and no molluscs or fish were found. The normal lack of surface flow in the lower reaches of the stream may prevent colonisation by fish present lower in the river system, whereas the steep, unstable bed of the stream and its irregular, sometimes torrential flow (Winterbourn 1976) may be the main reason for the lack of molluscs and paucity of filter-feeders.

The fauna of Middle Bush Stream can be compared with that of the larger Glentui River, which also flows through mountain beech in North Canterbury (Cadwallader 1975; M. J. Winterbourn, unpubl. data). The Glentui contains many more grazers, notably Ephemeroptera and sericostomatid caddisflies, more invertebrate predators including the megalopteran *Archichauliodes diversus* (Walker), and at least eight species of Rhyacophilidae, as well as large numbers of filter-feeders belonging to the trichopteran families Hydropsychidae and Polycentropodidae. Other abundant filter-feeders are larval Simuliidae and the mayfly *Coloburiscus humeralis* (Walker). It is also inhabited by the mollusc *Potamopyrgus antipodarum* (Gray) and five species of fish. On the other hand, the detritivores *Zelandopsyche ingens, Spaniocerca zelandica,* and species of Helodidae are absent or occur in very small numbers in the Glentui.

The lower zootic and ecological diversity of the Middle Bush Stream community may be primarily a function of the small size of the stream, its steep, unstable channel, and the presence of an almost closed forest canopy which reduces light penetration. Thus, the stream community is highly dependent on large, particulate, allochthonous material as its main source of energy (food), whereas larger forest streams like the Glentui have a more heterogeneous energy base in which coarse detritus plays a less important role but seston, periphytic algae, and bacterial films assume greater importance. In addition, larger, more stable streams should provide a greater diversity of well differentiated biotopes supporting a more diverse fauna.

Results of the tray experiments indicated that the more abundant insect species were broadly distributed among the biotopes considered. Ulfstrand (1967) has contended that the microdistribution of stream benthos is more closely related to food than to any other factor, and since similar amounts of detritus occurred in trays in the different biotopes the distribution of detritivores was unlikely to have been restricted by food availability. However, it was surprising to find generally weak correlations between animal numbers and detritus biomass, in contrast to the findings of other workers, e.g., Egglishaw (1964, 1969). The reason for this may be that a 'superabundance' of plant detritus relative to the numbers of available colonisers occurs in the stream, or that biomass is a poor indicator of food quality.

The composition of the fauna present in trays compared with that in samples of detritus and stones taken directly from the stream bed deserves some comment, since the representativeness of the former type of sample has been questioned – e.g., Mason (1976). Although direct comparisons between the stream and tray samples cannot be made, since they were taken in different years and the trays contained both stones and detritus, some general observations can be made. Clearly, the turbellarian *Neppia montana* was considerably overrepresented in trays (Table 6), where it occupied the undersurface of large, clean stones. However, if *N. montana* is excluded from the comparison (Table 6, column 4) the percentage contributions of most of the more abundant species are intermediate between those found in samples of stones alone and detritus alone, as would be predicted. Thus, the fauna which colonised trays appears to be fairly representative, although, as found by Hughes (1975), trays can also provide particularly favourable sites for some species.

The most notable feature of the insect life histories investigated in Middle Bush Stream was the general lack of seasonality (sensu Hynes 1970) exhibited; larvae and nymphs in a wide range of size classes were present in most months. This made it difficult or impossible to follow the growth of distinct cohorts of all species except *Zelandopsyche ingens, Zelandobius confusus*, and *Z. furcillatus*, in which growth was more closely synchronised.

Pupation or emergence was noted in at least 4 months for 8 of the 11 species considered; adults of *Spaniocerca zelandica* and *Hydrobiosella stenocerca* were taken in 8 and 9 calendar months respectively. Adults of most species first appeared in September or October, when the mean water temperature had risen to 7–9°C, but *Z. ingens* and *Stenoperla prasina* occurred only in late summer and autumn. *S. prasina* emerged earlier (November–February) in a lowland Canterbury stream (Winterbourn 1974), which indicates that the timing of the annual cycle may be affected by altitude (temperature).

Non-seasonal or poorly synchronised annual cycles and long flight periods have been described by Towns (1976) and Norrie (1969) for the majority of Ephemeroptera and Trichoptera in a northern New Zealand stream, and further examples are given by Winterbourn (1974), Devonport & Winterbourn (1976), and Hopkins (1976). A similar lack of seasonal rigidity in growth and emergence has been described by Hynes & Hynes (1975) for a large number of Australian stoneflies and by Illies (1969), who noted that the flight periods of many insects in South American montane streams were relatively greater than those of comparable species in Europe and North America.

Illies (1969) also pointed out that in South America many genera (life forms) of stream insects were represented by a few widely distributed species occupying wide ecological niches. He attributed this to the relative lack of isolation and subsequent endemic speciation during the Quaternary, and concluded that the less diverse Neotropical montane fauna displays the 'normal' picture, whereas the European and Nearctic faunas have become overdifferentiated so that species are crowded into narrowing niches. Present knowledge of the Australasian mountain stream faunas indicates that they conform to the South American pattern, and suggests that low species differentiation and ecological flexibility are the rule in the southern lands.

Table 5. Significant correlations found between numbers of invertebrates and the biomass of detritus in colonisation trays in 3 months

	$P<0.05$	$P<0.01$	$P<0.001$
	COARSE DETRITUS		
Sept.	Helodid Sp. A	Total fauna *Zelandopsyche*	
Nov.		Total fauna *Spaniocerca*	Helodid Sp. A *Olinga*
Feb.	Total fauna		*Spaniocerca*
	FINE DETRITUS		
Sept.	*Spaniocerca*	Total fauna *Deleatidium*	
Nov.	*Spaniocerca*	*Deleatidium*	Total fauna
Feb.	Total fauna	*Spaniocerca*	

Table 6. Relative abundance (%) of the more frequently occurring species taken in colonisation trays in September, November, and February 1974–75 and from samples of stones and detritus collected in the same months in 1973–74 (—, nil)

	Detritus	Stones	Trays	Trays (excl. *Neppia*)
Nesameletus sp.	1.0	6.3	4.4	5.7
Deleatidium spp.	11.0	55.0	17.4	22.6
Austroperla cyrene	4.3	1.0	3.2	4.2
Zelandobius furcillatus	1.0	5.0	—	—
Zelandobius confusus	9.6	8.0	1.0	1.2
Spaniocerca zelandica	33.6	6.0	11.0	14.3
Zelandopsyche ingens	9.6	1.0	6.8	8.8
Philorheithrus agilis	2.6	1.0	7.5	9.7
Hydrobiosella stenocerca	1.0	5.3	2.8	3.6
Olinga feredayi	3.0	2.0	5.9	7.7
Neppia montana	1.0	1.0	23.2	—
Eiseniella tetraedra	4.3	1.3	6.6	8.6

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