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Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream

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SUMMARY. The macro-invertebrate fauna of Waitakere River and its tributaries, a northern New Zealand kauri forest stream, was surveyed in January 1974 and January and June 1975, as part of a study on stream community dynamics. This survey and regular samples in the study area provided 144 taxa, almost three times the maximum number previously recorded from a New Zealand stream. Many species were restricted in distribution to a high gradient tributary, or the low gradient mainstream. These did not follow the division into rhithron and potamon families suggested for New Zealand.

Introduction

The structure and function of lotic invertebrate communities in the temperate Northern Hemisphere has received considerable attention, particularly those in streams with deciduous forest cover (review in Hynes, 1975). Leaf fall from these forests provides a seasonally changing habitat which in streams is occupied by many invertebrate species (Egglishaw, 1968; MacKay & Kalff, 1969). These communities may show fluctuations in the degree of heterotrophy corresponding to seasonal change in forest canopy development (Hall, 1972; Hynes, 1975).

In contrast, New Zealand streams, in their natural state, drain evergreen forests. The meagre evidence so far available suggests that litter fall varies from virtually non-seasonal in lowland rainforest (Daniel, 1975) to seasonal in southern beech forest (Winterbourn, 1976). Little is known of the structure and function of stream invertebrate communities in these forest habitats.

The following account is part of a 3-year study on the dynamics of benthic invertebrate communities in the Waitakere River, a northern New Zealand kauri forest stream.

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This is the first study of a New Zealand stream in the natural forest habitat, where an attempt has been made to treat the entire macro-invertebrate community at species level. Most previous studies have been concerned with specific taxonomic groups (reviews by Stout, 1973; Wise, 1973), invertebrates relevant to fisheries (e.g. Allen, 1951; Burnet, 1969; Hopkins, 1970; Cadwallader, 1975) or are restricted to a particular time of year. They have been hampered also by a lack of definitive taxonomic work.

This report describes the longitudinal changes that occur in faunal composition of the benthic community, and is based upon surveys of the Waitakere River and its two main tributaries.

An account of lesser known groups obtained during the study (Towns, 1978a, b), details of life histories and the possible effects of algal blooms on the communities will be published elsewhere.

Kauri forest is an informal term for mixed broadleaf podocarp forest in which kauri (*Agathis australis* Salisbury: Araucariaceae) is locally dominant in large stands. It is a forest unique to northern New Zealand, north of 38° S (Godley, 1975), and is one of several New Zealand forest types ecologically comparable to lowland tropical rainforest in structure (Dawson & Sneddon, 1969), although the climate is essentially temperate.

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Study area

The Waitakere River is a small coastal stream system (catchment area 34 km^2) which erodes Miocene andesite or andesitic sediments. In its upper catchment, the river flows over an eroded conglomerate peneplain, the edge of which forms falls in the 'Upper Waitakere Stream' (informal name) and the Cascade Stream. A dam on the Waitakere Falls restricts flow in part of the Upper Waitakere Stream to a few weeks each year. From its confluence with the Cascade Stream the Waitakere River flows westwards into a large coastal swamp (Fig. 1).

Minor tributaries (20 cm–1 m wide) in the Waitakere catchment flow between deeply incised banks and have a substrate of fine sand and gravel. In forested areas the watercourse is often completely overgrown.

The Cascade Stream, one of two major tributaries studied, has a high gradient (Fig. 2), consists of short (10–12 m) alternating pools and riffles, and ranges in width from 2–5 m. The substrate varies from conglomerate bedrock forming narrow channels, cascades and waterfalls, to cobbles in a matrix of very coarse sand. The second major tributary, the Upper Waitakere Stream, has a low gradient (Fig. 2) and varies from riffles 2 m wide and 10 cm deep, to pools 10 m wide and 2 m deep. The substrate is mainly of cobbles and pebbles, but in some areas is formed from bedrock.

The Waitakere River is of low gradient (Fig. 2) and 4–6 m wide for most of its course. Boulders and cobbles dominate in riffle substrates and extensive bedrock areas form channels and the base of pools. In the lower reaches (below site l) mud and clay more commonly form the stream basement.

Vegetation in the upper catchment (above site g) consists of relatively untouched mixed broadleaf-podocarp rain forest with large mature or regenerating stands of kauri, producing a canopy and subcanopy dominated by woody leaved trees and shrubs, and tree-ferns.

Below site g the Waitakere River flows through stock-grazed scrub (including regenerating mixed broadleaf-podocarp and kauri forest) and into more open, farmed areas.

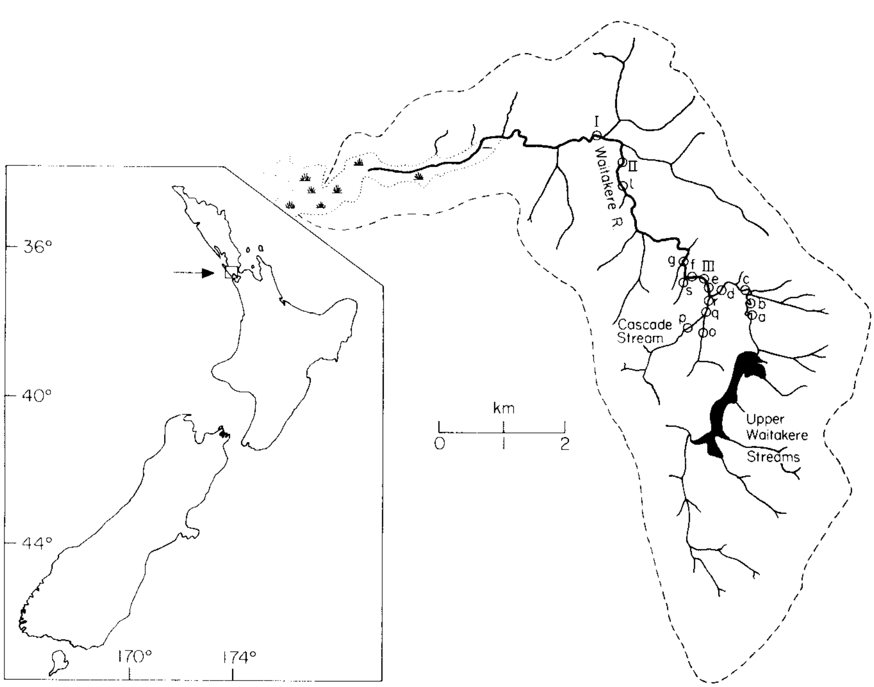

FIG. 1. Location of study area (inset, arrow) and study sites. Waitakere River catchment area, broken lines; Waitakere Reservoir shaded. Lettered sites, survey sites; Roman numerals, intensive (1-year) study sites.

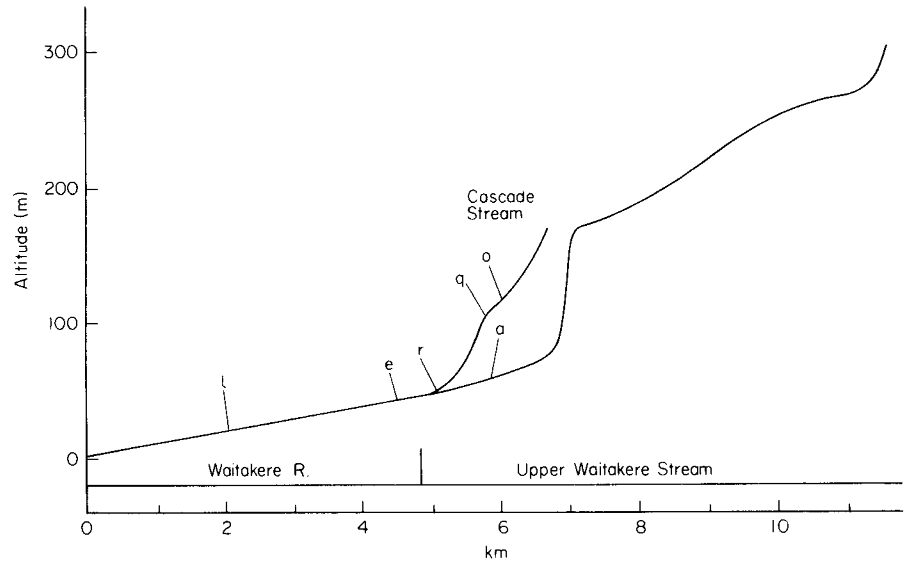

FIG. 2. Profile of the Waitakere River (as far down stream as site I) and the Upper Waitakere and Cascade Streams.

Emergent aquatic and semiaquatic macrophytes mainly were restricted to the lower Waitakere River, where the substrate was of mud and clay.

A variety of filamentous algae formed blooms which blanketed the substrate of fast flowing areas mainly during spring and summer (November–February) at forested sites (including the Waitakere River, Upper Waitakere Stream and cascades in the lower Cascade Stream), and throughout the year, although most widespread in summer, in farmed areas (lower Waitakere River). Bloom composition was variable with *Oedogonium, Cladophora, Melosira, Palmella, Spirogyra* and *Oscillatoria* the dominant genera.

Daytime spot water temperatures ranged from 10.5°C (August) to 23.0°C (January), and approximate the values obtained by McLean (1970) for the same area. During summer the Cascade Stream and other smaller tributaries were up to 5°C cooler than the Upper Waitakere Stream or the Waitakere River.

Analyses of water from several sites in the Waitakere River and its tributaries (January–December 1974, and in July 1975 and February 1976) indicate that the waters are slightly basic (pH 6.7–8.3), low in calcium (usually < 8 g m^{-3}), and intermediate between soft and medium hard (alkalinity 0.28–0.88 m-equiv. l^{-1}). However, they were comparatively rich in silica (14–35 g m^{-3}), sodium (17–25 g m^{-3}) and chloride (25–39 g m^{-3}).

There is no evidence that the algal blooms could be attributed to pollution or nutrient runoff.

Methods

Longitudinal variations in species composition were investigated initially by a kick-sample survey at regular (400 m) intervals, from minor tributaries to the Waitakere River at site I (Fig. 1). Each kick sample took 1 min to collect and two samples were taken at each site.

All sampling was centred on riffles, a biotope recognizable throughout the catchment area. Samples were obtained from the Cascade Stream (sites a–d), the Waitakere River (sites e–I) and a small (20–50 cm wide) runnel which represented a typical permanently flowing minor tributary (site s). The survey was carried out in January 1974, but the runnel was sampled in January 1976. Because samples obtained from the lower Waitakere River contained extremely dense algal growths, only those from site g were sorted. For the same reason kick samples at sites I and II were discarded and replaced by three Surber samples obtained at each of sites I and II in the same month (these also contained large quantities of filamentous algae).

Following the survey, five areas which represent different types of community structure were re-sampled by Surber sampler. These were the runnel (s), the Upper Cascade Stream (q), both in forest; and three types of main stream site as represented by site III (forest), site 1 (farmed, but under a canopy of the introduced conifer, *Cupressus* sp.) and site II (open farmland). Each site was sampled in January 1975 (summer) and June 1975 (winter), to provide information on seasonal changes in standing crop (number per unit area), species richness and diversity.

Surber samplers used were 20 x 20 cm (0.04 m^2) with a mesh of 200 μm. Kick samples were obtained with a 30 x 30 cm dip net, with 200 μm mesh.

Benthic samples were preserved entire and later separated from gravel by the sucrose flotation method of Anderson (1959), except for snails and caddisflies which were sorted directly from the gravel.

The use of Surber samples for community analysis has received considerable debate (reviewed in Bishop, 1973). It is probable that quantitative analysis requires up to twelve samples per site (Chutter, 1972; Allan, 1975), but this restricts the number of sites that can be sampled. As a compromise I have followed Needham and Usinger (1956) and Maitland (1964) in taking three samples per site. These are pooled to avoid the effects of selectivity by the sampler and species aggregations.

Results

The largest number of invertebrate taxa recorded for a New Zealand stream is fifty (Hopkins, 1970), considerably less than for most Northern Hemisphere studies. However, over the 3-year study period, the Waitakere River and its tributaries provided 144 taxa (see Towns, 1978a), a figure comparable with studies on similar sized streams in North America and Europe (Hynes, 1961; Minckley, 1963; Minshall, 1968; Ulfstrand, 1968b; MacKay, 1969; Coffman *et al.*, 1971; Fahy, 1975), but less than has been recorded in streams in the humid tropics (Bishop, 1973). The small number of species obtained elsewhere in New Zealand is probably partly due to imprecise identification and partly the result of poor taxonomic coverage of many groups.

Downstream changes in relative abundance of the dominant invertebrate groups are given in Fig. 3. A notable feature is the predominance of mayflies in all samples from the Cascade Stream and runnel. In most areas they consisted of Siphlonuridae (mainly *Coloburiscus humeralis* (Walker) and *Nesameletus* sp.) and Leptophlebiidae. Relative abundance of both families declined downstream, although Leptophlebiidae were considerably more abundant than siphonurids at most sites. A large proportion of the leptophlebiids were unidentifiable early instar nymphs, and were probably mainly *Deleatidium lillii* Eaton (Fig. 3).

Minor groups which showed longitudinal changes in abundance were Coleoptera (mainly Elmidae, Fig. 3) and Plecoptera. The latter occurred as more than 5% of the total fauna only in the runnel. Aquatic amphipods had a disjunctive distribution, with one eusirid species (*Paraleptamphopus subterraneus* (Chilton)) in the runnel, and the second, (*Paracalliope fluviatilis* (Thomson), Fig. 3) in the lower Waitakere River. The hydrobiid snail, *Potampopyrgus antipodarum* (Gray), also was most abundant in the lower Waitakere River (Fig. 3).

The sericostomatid caddisflies, *Baraeoptera roria* Mosely and *Pycnocentrodes* spp, and the chironomids, *Austrocladius* sp and *Paratanytarsus agameta* (Forsyth), were notable for their local abundance in the Upper Waitakere Stream and Waitakere River. These species appeared to be most abundant in areas susceptible to periphyton blooms.

A more detailed comparison of the distribution of fifty-two invertebrate species (Table 1) enables the fauna to be divided into three groups; species distributed throughout the system, and species restricted to either the tributaries or the mainstream.

A number of insect families, particularly trichopterans, contained different tributary and mainstream species (Table 1). The most marked distributional differences were for seven Sericostomatidae, three of which were tributary species (*Pycnocentria funerea* McLachlan, *Conuxia gunni* (McFarlane) and *Confluens hamiltoni* (Tillyard)), three were

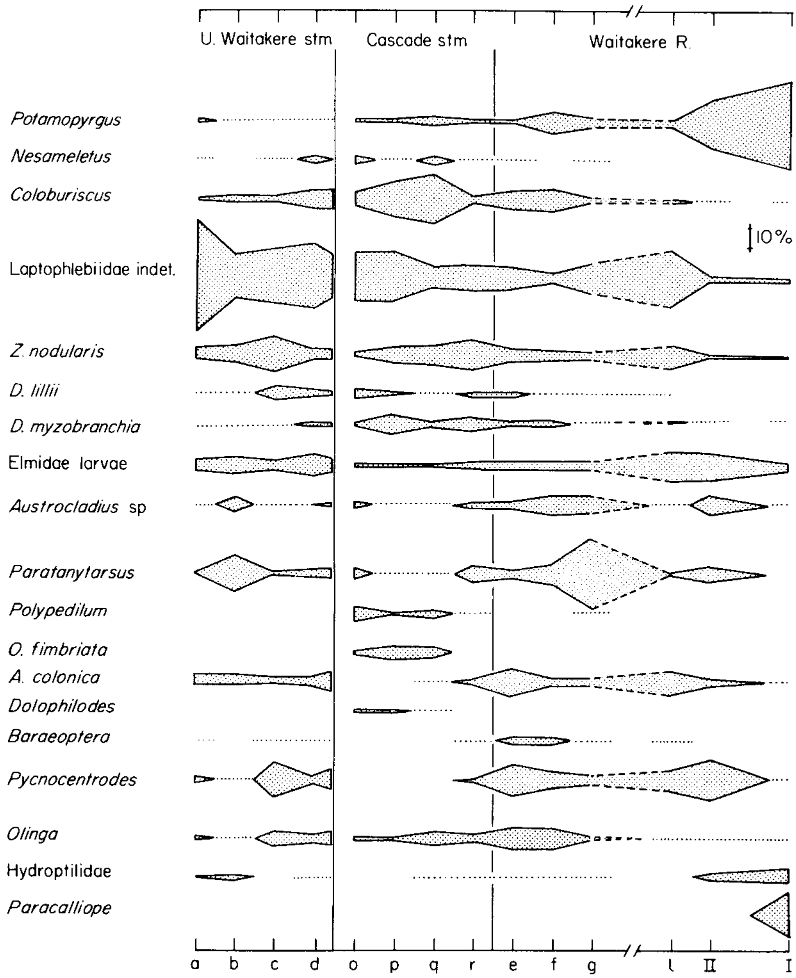

FIG 3. Longitudinal changes in relative abundance of the more common invertebrate species of the Waitakere River and its tributaries, from kick or Surber samples at sites a–I. Dots, < 1% of total; broken lines, sites discarded due to extensive algal cover.

mainstream species (*Pycnocentrodes* spp, *Pycnocentria evecta* McLachlan and *Baraeoptera roria*) and one was distributed throughout (*Olinga feredayi* (McLachlan)).

Similar distribution differences occurred for the chironomids *Polypedilum opimus* (Hutton), *Paratanytarsus agameta* and *Austrocladius* sp. (Fig. 3) and the hydropsychid caddisflies *Orthopsyche fimbriata* (McLachlan) and *Aoteapsyche colonica* (McLachlan) (Fig. 3). The restriction of *O. fimbriata* and the philopotamid *Dolophilodes mixta* Cowley mainly to cool tributaries (Fig. 3) was found also by Hopkins (1971) in the southern North Island.

With downstream changes in species composition, a parallel change occurred in the number of insect families obtained at each site. These increased from nine in the runnel to twenty-three to twenty-five in Cascade Stream tributaries. Between sixteen and twenty-one families were found in the Cascade Stream, Upper Waitakere Stream and most of the Waitakere River, but only eleven at site I. A similar change occurred in the number of trichopteran families present; from one (Hydropsychidae) in the runnel to seven or eight in the Cascade Stream tributaries and four at site I. Families found only in the Cascade Stream and its tributaries were

TABLE 1. Distribution of fifty-two invertebrate species in the Waitakere River and its tributaries. Species confined to tributaries are enclosed by dashed lines, marked a; species confined to mainstreams are enclosed by dashed lines in b. +, >5 per sample; –, <5 per sample. Species surrounded by the solid line were not obtained during the survey in January 1974.

		Runnel	Cascade Stream				Upper Waitakere Stream					Waitakere River				
Family	Species		(o)	(p)	(q)	(r)	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(1)	II	I
Leptophlebiidae	*Zephlebia dentata* (Eaton)	+														
Eusiridae	*Paraleptamphopus subterraneus* (Chilton)	–														
Notonemouridae	*Halticoperla viridans* McLellan & Winterbourn	–	a													
Ephemeridae	*Ichthybotus hudsoni* (McLachlan)	–	–		–											
Hydropsychidae	*Orthopsyche fimbriata* (McLachlan)	+	+	+	+											
Planariidae	*Neppia montana* (Nurse)	–	–	–	+	–	–									
Tipulidae	*Hexatomini* indet.	–	–	–	–	–				–	–	–				
Leptophlebiidae	Gen. et. sp. nov.	–	+	+	+	+	+		–			–				–
Ptilodactylidae	Gen et sp. indet.	–		–	–		–	–		–	–		–	–		
Chironomidae	? *Austrocladius* sp.	–	+	+	+	+	–	+	–	–	+	+	+	+	+	
Leptophlebiidae	*Deleatidium myzobranchia* Phillips	–	+	+	+	+	–		+	+	+	+	+	+	+	–
Leptophlebiidae	*Zephlebia nodularis* (Eaton)	–	+	+	+	+	+	+	+	+	+	+	+	+	+	–
Hydrobiidae	*Potamopyrgus antipodarum* (Gray)	–	+	+	+	+	–	+	+	+	+	+	+	+	+	+
Siphlonuridae	*Coloburiscus humeralis* (Walker)	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–
Elmidae	*Hydora nitida* Broun		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sericostomatidae	*Olinga feredayi* (McLachlan)		+	+	+	+	+	–	+	+	+	+	+	+	+	–
Simuliidae	*Austrosimulium australense* (Schiner)		+	+	+	–	+	+	–	–	–	–	–	–	–	–
Corydalidae	*Archichauliodes diversus* (Walker)		+	–	+	–	–	+	–	+	–	–	+	+	–	–
Hydraenidae	*Orchymontia* sp.		–	–	–	–	–	+	–	+	+	+	–	+	–	–
Chironomidae	*Paratanytarsus agameta* (Forsyth)		+	–	+	+	+	+	+	+	+	+	+	+	+	
Hydraenidae	Genus II sp. A		–	–	–	–	–	–	–	–	–		–	+	–	
Leptophlebiidae	*Zephlebia* sp.		–	–	–		–	+	+	–	–	–	+		–	
Leptophlebiidae	*Atalophlebioides* sp. A		–		–	–			–	–	–	+	–	+	–	
Leptophlebiidae	*Deleatidium lillii* Eaton		+	+	–	+	–	+	+	+	+	–	+	–		

Leptophlebiidae	*Deleatidium* sp. C	+	+	−	−	−		+		+	−	−	−		
Tipulidae	*Limoniini* indet.	−	−	+	−	−	−		−	+	−	−	+		
Rhyacophilidae	*Hydrobiosis parumbripennis* McFarlane	−	−	−	−				−	−	−	−	−		
Eustheniidae	*Stenoperla prasina* (Newman)	+	−	−	−	−		−	−	−	−	−			
Siphlonuridae	*Nesameletus flavitinctus*	+	−	+	+	−		−	−	−		−			
Chironomidae	*Polypedilum opimus* (Hutton)	+	+	+	+		−			−		−			
Rhyacophilidae	*Hydrobiosis clavigera* McFarlane	−	−	−	−			−	−	−	−				
Leptoceridae	*Triplectides obsoleta* McLachlan	−	−			−	−		−						
Hydraenidae	Genus III sp.	−	−	−	−			−							
Philopotamidae	*Dolophilodes mixta* Cowley	+	+	+											
Helicopsychidae	*Helicopsyche albescens* Tillyard	−	−		a										
Helicophidae	*Zelolessica cheira* McFarlane		−	−											
Sericostomatidae	*Conuxia gunni* (McFarlane)			+											
Leptophlebiidae	*Atalophlebioides* sp. B				+										
Leptophlebiidae	*Deleatidium* sp. E				+										
Sericostomatidae	*Confluens hamiltoni* (Tillyard)				+										
Hydropsychidae	*Aoteapsyche raruraru* (McFarlane)				+										
Hydroptilidae	*Oxyethira albiceps* (McLachlan)			−	−	+	+		−	−	−	−		+	
Hydropsychidae	*Aoteapsyche colonica* (McLachlan)			−	+	+	+	+	+	+	+	+	+	+	
Leptoceridae	*Hudsonema amabilis* (McLachlan)				−	−		−	−	−		−			
Sericostomatidae	*Baraeoptera roria* Mosely				−	+		+	−	+	+	+	−		
Sericostomatidae	*Pycnocentrodes modesta* Cowley + *aeries* Wise				+	+	−	+	+	+	+	+	+	−	
Hydraenidae	Genus II sp. B					−	−		−						
Tetrastemmatidae	*Prostoma ? graecense* (Bohmig)						−		−			−	+	−	−
Siphlonuridae	*Rallidens mcfarlanei* Penniket							−	+			−	−		
Planariidae	*Cura pinguis* (Weiss)														
Eusiridae	*Paracalliope fluviatilis* (Thomson)									b					+
Planariidae	*Neppia* sp.													−	

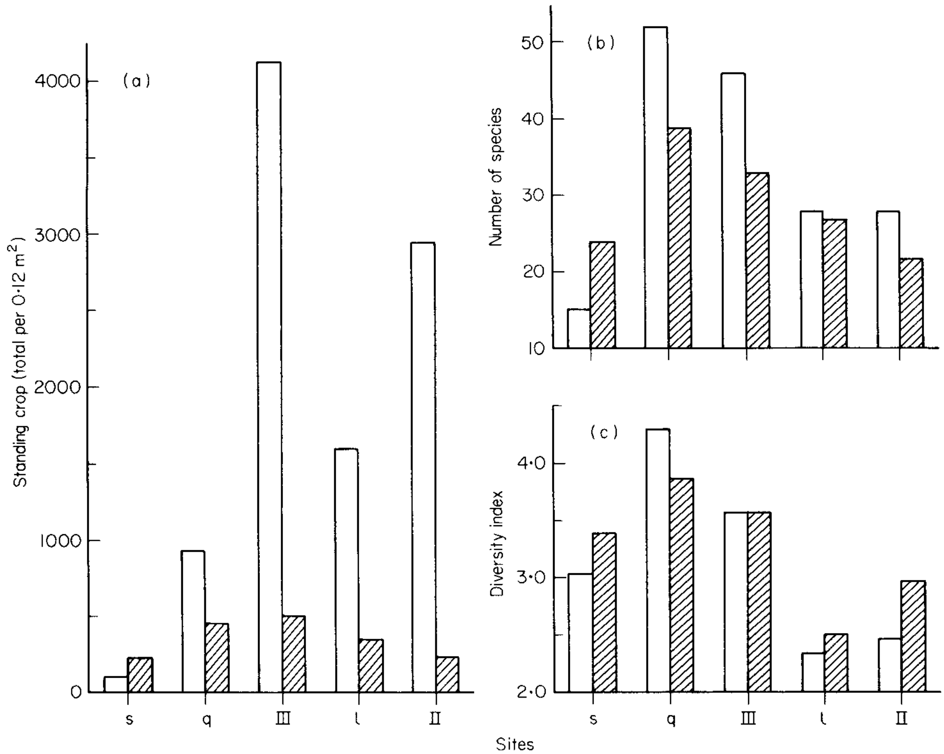

FIG. 4. Benthic standing crop (a), species richness (b), and diversity index (c) in summer (unshaded) and winter (shaded) at five Waitakere sites arranged in order of increasing discharge: s, runnel; q, upper Cascade Stream; III, Waitakere River in forest; I, Waitakere River under *Cupressus* canopy; II, Waitakere River in farmed area. All sites sampled in January 1975 (except runnel; January 1976) and June 1975, with three Surber samples per site.

Philopotamidae, Helicophidae and Helicopsychidae.

Changes in standing crop, species richness and diversity at five sites Surber sampled in 1975 are presented in Figs. 4a, b, c. Richness declined in downstream sequence from a maximum in the Cascade Stream, while standing crop increased from a minimum in the runnel.

Combination of numbers of species and allotment of individuals per species (Shannon-Weaver diversity index), is given in Fig. 4c. The low summer diversity of sites in farmland (I and II) is associated with the high standing crop and low species richness in these sites during the periods of maximum algal cover.

The tendency for stream invertebrates to form different associations within watersheds is well documented, particularly for the Northern Hemisphere (references in Hynes, 1970). This has been formalized by Illies (1961) and Illies and Botosaneanu (1963), who defined zones subdivided by temperature, substrate and faunal composition.

The only Southern Hemisphere streams to which this scheme has been applied in detail are in South Africa (Harrison, 1965; Chutter, 1970). Bayly & Williams (1973) have attempted to apply the system to Australasian streams, by replacing Northern Hemisphere families typical of particular zones with their probable Australasian counterparts. However, because a number of families given by Bayly & Williams (1973) are absent from New Zealand, and several others were not susceptible to capture, their modified system was difficult to apply to the Waitakere watershed. Of the families represented in the Waitakere system, only two rhithron families, as defined by Bayly & Williams (Helodidae and Philopotamidae), were restricted in distribution. Both occurred in the tributaries (e.g. Cascade

Stream). Only one potamon family, Hydroptilidae, was rare in the tributaries, but abundant in the main stream. Six 'rhithron' families of Bayly and Williams were abundant throughout (Leptophlebiidae, Gripopterygidae, Simuliidae, Elmidae, Hydraenidae and Rhyacophilidae), as were three 'potamon' families (Siphlonuridae, Chironomidae and Leptoceridae). One potamon family, Siphlonuridae, was most abundant in the headwaters.

Physically, the forested Waitakere River and its tributaries resemble the rhithron in character. However, the wide spread of both rhithron and potamon families throughout the system suggests that the Illies and Botosaneanu scheme, in its present form, may not be applicable to New Zealand streams.

Discussion

New Zealand stream invertebrate communities lack a number of families which are widespread elsewhere. These include asellid isopods and gammarid amphipods, the mayfly families Heptageniidae and Baetidae, Northern Hemisphere plecopteran families, and the caddisfly families Limnephilidae and Glossosomatidae (see Bayly & Williams, 1973; Stout, 1975).

Conversely, many common New Zealand groups are less diverse or absent in the Northern Hemisphere, e.g. the families Eustheniidae, Gripopterygidae, Austroperlidae (Bayly & Williams, 1973) and Notonemouridae (Illies, 1975) (Plecoptera), Leptophlebiidae and Siphlonuridae (Ephemeroptera), and Sericostomatidae (Trichoptera). In addition some are restricted to Australasia e.g. Oeconesidae (see Neboiss, 1975; Cowley, 1976) or endemic to New Zealand e.g. Latiidae (Mollusca) and Siphlaenigmatidae (Ephemeroptra) (Winterbourn, 1973; Penniket, 1962; Towns, 1978b).

With such a variety of distinctive elements, New Zealand ecological homologues have been suggested for well known Northern Hemisphere groups. *Gammarus* is considered by Stout (1975) to be replaced in New Zealand by the eusirid, *Paracalliope*, *Lymnaea* by *Potamopyrgus* (Stout, 1975) and Heptageniidae (= Ecdyonuridae) by Leptophlebiidae (Hynes, 1970; McLellan, 1975; Stout, 1975). This is misleading, because in addition to faunistic characteristics, there may be fundamental differences between southern evergreen forest streams and those of holarctic deciduous forest in the timing, composition and breakdown of allochthonous detritus. Consequently groups such as gammarid amphipods, associated with accumulations of soft deciduous leaf material (e.g. Minshall, 1967) probably have no single ecological counterpart in New Zealand. For example, the role of general scavenger and detritivore, which elsewhere is apparently filled by gammarids (and isopods), appeared to be occupied principally in open areas of the Waitakere River by the hydrobiid snail, *Potamopyrgus antipodarum*. In the forested areas, where *Potamopyrgus* was less abundant, fine particle feeders, such as sericostomatid caddisflies and leptophlebiid mayflies probably performed a similar function. It therefore seems to be more realistic to suggest that New Zealand families may have radiated to fill the niches occupied by more than one overseas 'equivalent' than to seek direct counterparts.

In most streams throughout the world, the largest number of species in the invertebrate fauna are comprised of Diptera, dominated by Chironomidae. Chironomids are relatively poorly represented in New Zealand, and this is reflected in the small number of species obtained from the Waitakere River. Diptera comprised twenty-four of the 144 Waitakere taxa, of which chironomids formed sixteen species (see Towns, 1978a). By comparison, Fahy & Murray (1972) obtained 54 chironomid species in a small stream in Ireland and Coffman (1973) obtained 143 chironomid taxa in a small stream in eastern North America.

In contrast, Trichoptera were particularly well represented in the Waitakere system (thirty-four species), and formed a much larger element than in many Northern Hemisphere streams (e.g. Hynes, 1961; Minckley, 1963; Ulfstrand, 1968a; Coffman *et al.*, 1971; Fahy, 1975). A similar number of species (thirty-nine) was obtained by Anderson & Wold (1972) from a stream in Oregon. The most diverse Waitakere families were Rhyacophilidae (six genera, eleven species) and Sericostomatidae (six genera, eight species).

The number of ephemeropteran species

found here (twenty-four, of which seventeen were Leptophlebiidae) is also high for a small area. In a survey of many European studies, Ulfstrand (1968a) found that the largest number of Ephemeroptera species collected in a single study was twenty-two, with most stream systems providing between fifteen and twenty. However, more recently Sowa (1975) obtained up to forty-two species of mayflies from rivers in the Polish Carpathians.

Plecopterans are often well represented in European rivers, with many workers obtaining fifteen to twenty-five species in a single stream (Ulfstrand, 1968a). North American streams may also have a large plecopteran fauna; forty-three species were collected by Kerst & Anderson (1974) from a stream in Oregon. In the Waitakere River as in most New Zealand streams (McLellan, 1975), this group was poorly represented (eight species). It is notable that representatives of all of the New Zealand stonefly families occurred in the cool Waitakere tributaries, and the most abundant mainstream species (*Acroperla trivacuata* (Tillyard) and *Zelandobius furcillatus* Tillyard) were common only during winter.

Longitudinal changes in composition of the Waitakere River communities and in standing crop, species richness and diversity, probably are linked with several physical differences between tributaries and mainstream. These include differences in temperature, slope and extent of algal cover. Associated with these are changes in the trophic structure of the invertebrate communities from a predominance of collector-microgatherers in the headwaters, to scrapers in the farmed areas (categories of Cummins, 1974, 1975). Such trophic differences closely resemble the change from primarily heterotrophic tributaries to an autotrophic mainstream as outlined by Cummins (1974, 1975). The tendency towards increased heterotrophy and hence maturity (Fisher & Likens, 1973) in the cool, forested geologically immature tributaries has been found elsewhere by Minckley (1963), Fisher & Likens (1973) and Bishop (1973).

Despite suggestions that the aquatic fauna of New Zealand generally has a low species diversity (Davis & Winterbourn, 1977), the number of species obtained during the present study approximates the species richness found from similar studies in the Northern Hemisphere. However, many common Northern Hemisphere families are notably absent from the New Zealand fauna, which tends to be mayfly and caddisfly rich, but chironomid and stonefly poor. It is therefore possible that invertebrate families in the Waitakere system did not fit the zonation scheme proposed for Australasian streams (Bayly & Williams, 1973) because many families present in New Zealand have radiated into a wider range of habitats there than elsewhere.

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