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The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river

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Summary

The life history, feeding relations and production of the stonefly *Stenoperla prasina* were studied for 16 months in the Selwyn River, South Island, New Zealand. Larval life is about 1 year with growth occurring in all months. Although emergence of adults was observed only from November to February, egg hatching probably occurred over an extended period as small larvae were present in most months. Larvae were mainly carnivorous except in early instars when most guts contained detritus. Larvae of a mayfly, *Deleatidium* sp. and a chironomid, Orthocladiinae sp. were the most important prey items. In April of two successive years the guts of most stoneflies examined were filled with diatoms (*Gomphonema* sp.) and filamentous algae which were abundant in the river only at these times. Algal feeding was not found in other months.

Larvae of the main prey species, *Deleatidium*, were present in all months, being most abundant in summer and declining in numbers during winter. Maximum emergence occurred in March and April. The annual cycle of *Deleatidium* was difficult to interpret as larvae of all sizes were present in all months. Two generations probably occurred in a year, a fast-growing summer generation and a slower-growing and less synchronized winter generation.

Mean annual standing biomass, annual production and turnover ratios (P/B) were calculated for both species. The latter were within the range of values given by Waters (1969) but may be subject to error from several sources. Shortcomings in the method used to estimate production are discussed.

Introduction

In recent years, stream ecologists have shown increasing interest in determining the trophic relations of benthic invertebrates as a necessary prerequisite to studying energy flow and community dynamics (Cummins, 1973). A few of these studies have been concerned with predacious insects, and have considered such things as interspecific competition, predator-prey size and density relationships, feeding in relation to prey availability, and temporal (e.g. life history) relationships (Davis & Warren 1965; Brocksen, Davis & Warren, 1968; Sheldon, 1969; Thut, 1969; Fahy, 1972).

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Trophic relations of benthic stream invertebrates have not been investigated in New Zealand, although the life histories of several insects have been studied (Glasgow, 1936; Hamilton, 1940; Wisely, 1961, 1962; Winterbourn, 1966; McLean, 1970), and comprehensive feeding studies have been made on a number of stream-dwelling fish (Allen, 1951; McDowall, 1965; Hopkins, 1970).

The present study was initiated in view of the proximity of a large and accessible population of *Stenoperla prasina* (Newman), a species of Eustheniidae which is considered to be one of the most archaic living plecopterans (Illies, 1965). *S. prasina* is the only eustheniid occurring in New Zealand, although four genera are found in south-eastern Australia (Riek, 1970). The anatomy and external features of the adult stonefly and final instar larva have been described by Helson (1934) who also described the egg, hatching of the egg and two of the early larval instars (Helson, 1935.) The initial aim here was to investigate its life history and the food of the larvae, but later the study was extended to incorporate an examination of the life history and population changes of its main ephemeropteran prey. This was a species of *Deleatidium* (family Leptophlebiidae), the dominant mayfly genus in most New Zealand running waters. At the present time, specific identification of *Deleatidium* species cannot be made with certainty but the species considered here closely resembled *D. autumnale* Phillips.

Finally, an attempt was made to estimate production of both species using the method outlined by Hamilton (1969).

Study area

Fieldwork was carried out at Chamberlain's Ford on the Selwyn River, 30 km southwest of Christchurch in the South Island of New Zealand. The Selwyn rises in the foothills of the Southern Alps and flows eastwards across the Canterbury Plains for 60–80 km before entering Lake Ellesmere, a large brackish-water lagoon. The river can be divided into three parts on the basis of water flow; upper and lower sections where surface water is present throughout the year, and a middle section approximately 30 km long, where the river flows underground in summer. Physical conditions at eight points on the river have been described by Wisely (1962). The study area was located in the lower section where the river flowed in a well-established channel 5 m wide and up to 250 mm deep. The river bed consisted of rounded, greywacke pebbles,

Table 1. Mean particle size composition of loose surface and compacted basal sediments of the river bed as indicated by core sampling in December 1972. Each sediment fraction is expressed as a percentage of the total dry weight of bed material. Also shown are numbers of *Deleatidium* larvae found in the two layers

	Surface	Base
No. of cores	8	8
Pebbles (> 15·9 mm)	42·3	34·3
Gravel (2·8–15·9 mm)	49·9	48·9
Coarse sand (0·5–2·8 mm)	4·7	8·6
Very fine sand (0·063–0·50 mm)	3·1	8·2
No. of *Deleatidium* per core	9·9	0·25
($\bar{x}$ and range)	3–25	0–1

gravel and occasional stones up to 150 mm diameter, loosely packed over a compacted base. The upper layer of loose material averaged 100–150 mm depth. Particle size composition of the substratum is shown in Table 1. Gravel predominated in both upper and lower layers, but over twice as much sand was present in the compacted base. Current velocity and discharge were not measured regularly during the study, but general observations indicated that little seasonal variation occurred. Maximum flow rates at the sampling station were about 1 m s^{-1}. Morning water temperatures ranged from 7·5°C in July to 19°C in January, a range of 11·5°C (Fig. 1).

The river flowed through cultivated farmland in the study area and a row of willows (*Salix* spp.) lined the northern bank. Monkey musk (*Mimulus guttatus* DC.), water cress (*Rorippa microphylla* (Boenn.)) and duckweed (*Lemna minor* L.) grew along the river margins but no rooted macrophytes were present in the open water. In most months a thin film of diatoms and filamentous algae coated the upper surfaces of stones and pebbles but in February 1972 thick patches of *Oscillatoria* sp. occurred on stones near the banks and by mid-April had spread throughout the river. In April of both years a thick coating of diatoms, predominantly a species of *Gomphonema* was present, but it disappeared by mid-May.

The invertebrate community was dominated by larvae of three caddisflies, *Pycnocentrodes aureola* (McLachlan), *Olinga feredayi* (McLachlan) and *Hydropsyche colonica*, McLachlan, the mayfly *Deleatidium* sp. and a gastropod, *Potamopyrgus antipodarum* (Gray). Occurring in smaller numbers were two amphipods, *Phraetogammarus fragilis* Chilton and *Paracalliope fluviatilis* (Thomson), a siphlonurid mayfly *Coloburiscus humeralis* (Walker), the lumbricid *Eiseniella tetraedra* (Savigny), larval Chironomidae (mainly Orthocladiinae) and several species of carnivorous caddis belonging to the families Rhyacophilidae and Polycentropidae. *Stenoperla prasina* was the only stonefly present. The only vertebrate seen in the study area was the eleotrid bully, *Gobiomorphus basalis* (Gray).

Methods

Substrate analysis

Core samples taken from the stream bed in December with a 60-mm internal diameter corer were used to describe the physical composition of the substratum. They were also used to examine the vertical distribution of fauna within the substratum and its effect on the efficiency of biological sampling. Eight vertical cores were taken above the compacted basement material, and eight cores from this compacted layer after the overlying sediment had been cleared away as in Surber sampling. All samples were 100–150 mm deep. Invertebrates were removed from the cores and the sediments were dried and mechanically sorted into four size classes using the numbers 3 (15·90 mm), 6 (2·80 mm), 10 (0·50 mm) and 17 (0·063 mm) sieves of the Endecott series. These closely approximate the lower limits of the pebble, gravel, coarse sand and very fine sand categories of Cummins & Lauff (1969). The fine silt fraction was very small (< 1 %) and was ignored but the other fractions were weighed and expressed as a percentage of the total core weight.

Biological sampling

Bottom samples were taken from the same riffle in the middle of each month, from January 1971 to April 1972. On each occasion, six samples were taken with a Surber sampler (area 0·09 m^2; mesh aperture width 0·4 ± 0·05 mm) along a diagonal transect extending across the stream, all stones above the compacted basement layer being stirred, brushed and removed from within the sampling frame. Core sampling (Table 1) indicated that very few animals occurred below the level to which samples were taken. The efficiency of the sampler net in catching small *Deleatidium* larvae was tested by passing a bottom sample through the sampler net which was backed by a 0·2-mm mesh net. No larvae with head widths >0·44 mm, and few of 0·40 mm passed through the sampler net, but smaller larvae were inadequately collected. A non-quantitative sample was also taken with a hand net on each sampling day and adult stoneflies and final instar exuviae were obtained by searching and sweeping streamside vegetation. All collections were made between 09.00 and 12.00 hours and were preserved immediately with 10% formalin. As larvae of *Stenoperla* were believed to be nocturnal feeders (Helson, 1934), this should have ensured that food would be present in the foreguts of most larvae.

All samples were sorted twice in the laboratory, larvae of *Stenoperla* and *Deleatidium* being removed and all those of *Stenoperla* were measured. Measurements were made on subsamples of up to fifty *Deleatidium* from each sample (i.e. about 300 per month) obtained with a subsampler similar to that described by Mundie (1971). Head capsule width across the eyes and, on older larvae of both species, wing pad length from inner angle to wing tip, were measured with a linear eyepiece graticule at a magnification of ×25. All final and penultimate instar larvae of *Stenoperla* were sexed, females being recognized by the presence of a slight invagination surrounded by a dark patch on the eighth abdominal sternite. Eye dimorphism was used for sexing older larvae of *Deleatidium*.

As gut analyses were made on a proportion of the stonefly larvae each month, dry weights could not be determined directly. Instead, biomass was calculated from a regression line relating head width and dry weight in a sample of sixty larvae dried for 5 days at 65°C and individually weighed to the nearest 0·1 mg. A similar regression was obtained for *Deleatidium* (for use in estimating production) but because of their small size larvae were pooled into seven size groups for weighing. Monthly collections of *Deleatidium* larvae were also dried and weighed to determine total biomass. As these samples had been kept in 70% alcohol for variable periods prior to weighing, some loss of organic weight could be expected. To correct for this, fresh weight: dry weight ratios of newly collected larvae were compared with those of larvae kept in 70% alcohol for 30 days by which time they could be expected to have achieved a fairly constant weight (Howmiller, 1972). The average dry weight of preserved larvae was 73·3% that of fresh material, and biomass values were adjusted accordingly.

Gut analyses

Gut contents of twenty *Stenoperla* larvae were examined each month except in the first 4 months when larger numbers were analysed. Guts were dissected from measured larvae and their contents mounted on slides in lactophenol-PVA containing the stain Lignin Pink. Slides were examined under a compound microscope and gut contents identified as algae, animal remains (identified as accurately as possible) or detritus, which was defined as apparently structureless matter of unknown origin. Lengths of chironomid head capsules and *Deleatidium* tarsi were measured at a magnification of ×40. Intact *Deleatidium* head capsules were rarely found in stonefly guts but tarsi were often found, could be easily recognized, and conveniently, were of almost the same length on all legs of any one individual.

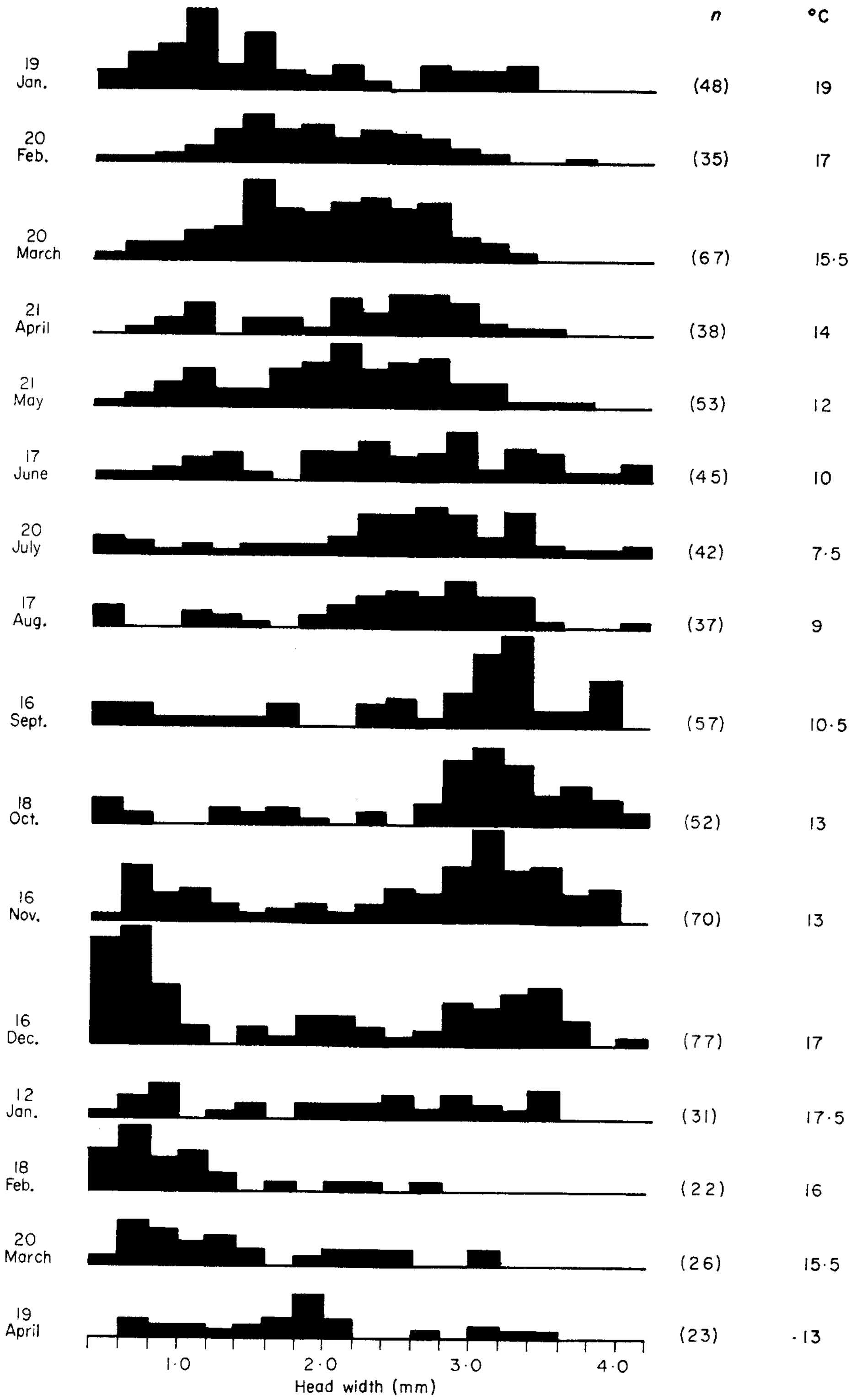

Fig. 1. Size frequency distribution of *Stenoperla* larvae taken in six Surber samples (0·54 m²) each month from January 1971 to April 1972. Sample sizes shown in brackets. Water temperatures at times of sampling also given.

Diel feeding experiment

To examine whether *Stenoperla* possessed a diel feeding rhythm larvae were collected at hourly intervals over a 24-h period. If a well-defined feeding rhythm existed it was hoped this would be expressed by the amount and position of food in the guts at different times. On collection, larvae were anaesthetized with CO_2 to prevent any possible regurgitation, and then preserved in 10% formalin. Later they were cleared in a strong solution of hot KOH so the position of the gut and its contents could be seen clearly. The length of gut containing food and the position of the food was measured under a dissecting microscope. Although volume of food present would provide a better index of gut fullness, length of gut containing food was thought to represent a useful approximation.

Life history and feeding of *Stenoperla*

Annual cycle

Although a wide size range of larvae was present each month, (Fig. 1), the general pattern of growth of the main component of the population could be followed. No first instar larvae or eggs were collected in field samples, but probable third instars were taken from November to March. Greatest numbers of small larvae were present in November and December, and these appeared to grow rapidly during summer and autumn, many reaching the penultimate (F-1) instar by winter. Further small larvae were recruited into the population in later months, perhaps coming from delayed-hatching eggs. Some F-1 larvae were present in all months except January 1971 and February of both years, with most occurring in winter and spring (Fig. 2). Final (F) instar larvae were found in seven calendar months, appearing first in June. Emergence was observed from November to February, with most final instar exuviae being found in December and January. These were mainly attached to leaves and stems of *M. guttatus* and *R. microphylla*, and occurred up to 150 mm above the water surface. Few

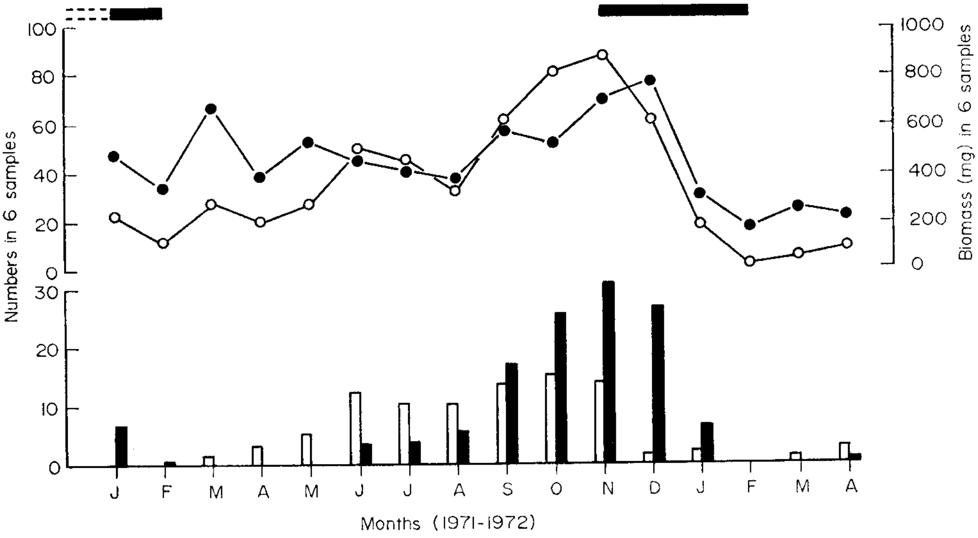

Fig. 2. Total numbers (●) and dry weights (○) of *Stenoperla* larvae taken in six Surber samples each month. Open columns show numbers of F-1 larvae; solid columns numbers of final instar larvae. The horizontal bars indicate the periods of adult emergence.

adults were seen in the field and nothing is known of their emergence or oviposition behaviour. The relatively long (7 month) period during which final instar larvae were found, contrasts with the much shorter (4 month) emergence period, and suggests that some synchronization of the life cycle occurs in the final instar.

Seasonal abundance

Numbers of larvae collected in the six samples each month ranged from seventy-seven in December 1971 to twenty-three in April 1972 (Fig. 2). Considerable variation was found between samples on any one day and is indicated by the high standard errors of the means which ranged from 14 to 54 % of each six sample mean. Numbers remained fairly constant over winter and were highest in November and December when many small larvae were entering the population, and not all mature larvae had emerged. The fairly constant population density over most of the year suggests that larval mortality was low. Certainly, mortality from predation was probably low as indicated by gut analyses of forty-one *G. basalis*, the only fish collected from the riffle, in which no stonefly fragments were found.

Stenoperla biomass increased gradually during the year from a minimum in February to a maximum in late spring. It then fell sharply as the insects emerged (Fig. 2).

Larval instars and sex ratio

Larval instars could not be distinguished using head width data, but the three largest instars could be recognized using head widths in combination with wing pad measurements (Table 2). In addition, female larvae could be distinguished in the two final instars by the dark depression on the eighth sternite. Considerable overlap in head widths of F and F-1 larvae was found, as well as marked sexual dimorphism, such that the mean head width of F-1 females was greater than that of F males. Mean head width increased from instar F-1 to F by a geometric increase factor of 1·11 and from F-2 to F-1 by 1·19. If it assumed that larval growth of *Stenoperla* conforms with Dyar's Rule and a growth increase factor of 1·19 is employed (Holdsworth, 1941, showed that the increase in size from F-1 to F may be atypical), then fifteen larval instars would occur.

Larvae of both sexes were collected in almost equal proportions, 49·6% of the 351 F and F-1 larvae taken during the study being females.

Food of larvae

In the Selwyn River, larger larvae were mainly carnivores, whereas the guts of most small larvae contained detritus (Table 3). Some large larvae also contained detritus,

Table 2. Head widths and wing pad lengths of the three largest larval instars of *Stenoperla*

Instar	Sex	No. measured	Head widths (mm) $\bar{x}$	Head widths (mm) Range	Wing pad lengths (mm) $\bar{x}$	Wing pad lengths (mm) Range
F	♂	66	3·10	2·52–3·44	2·74	2·40–3·16
F	♀	70	3·60	2·88–4·12	3·22	2·68–3·64
F-1	♂	70	2·79	2·32–3·08	1·04	0·64–1·16
F-1	♀	56	3·22	2·76–3·72	1·12	0·96–1·32
F-2	Unidentified	76	2·54	2·20–2·84	0·50	0·40–0·64

Table 3. Percentage occurrence of different food items in the guts of five size classes of *Stenoperla* larvae. These represent all 1971 samples (excluding those containing algae in April) combined

Size classes (head width mm)	No. of larvae	Percentage of larvae containing four foods			
		Deleatidium	Chironomidae	Detritus	Other
<1·20	26	3·5	7·5	89	0
1·20–1·90	104	57	5	20	17
1·90–2·60	92	58	11	14	18
2·60–3·30	96	70	20	2	8
>3·30	38	53	37	2	8

much of which may have been derived from the guts of prey organisms. The number of larvae with empty guts was determined in the first 7 months of the study only, during which 383 individuals were dissected. Of these 27% were empty, with a maximum of 36% in January.

Seasonal variations in diet are shown in Fig. 3. In most months *Deleatidium* larvae were the most frequently occurring food items and overall were present in 65% of the larvae containing food. In some months chironomid larvae (mainly Orthocladiinae) were also important and in May more *Stenoperla* larvae contained chironomids than mayflies. Other foods and their frequency of occurrence are given in Table 4. No instances of cannibalism were found.

Most stoneflies which had been feeding on *Deleatidium* contained fragments of only a single larva. In fact, of 244 containing *Deleatidium* only ten contained recognizable parts of two mayflies and only two contained fragments of three. Unless they were very small, it appeared from examination of gut contents that mayfly larvae were rarely ingested whole. Rather, it seems they are first torn apart by the mouthparts and only partially ingested. Stonefly larvae observed in the laboratory behaved in this way. By contrast, large numbers of chironomid larvae were ingested whole by some stoneflies (Table 5).

Size relationships of stoneflies and their mayfly and chironomid prey are shown in

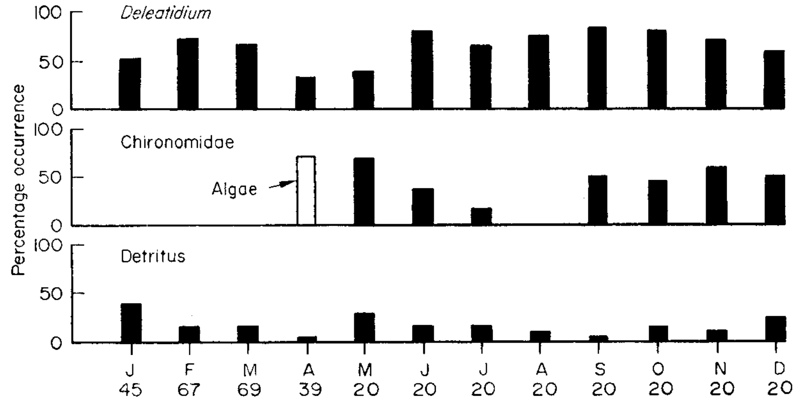

Fig. 3. Percentage of *Stenoperla* larvae dissected each month containing fragments of *Deleatidium* larvae, chironomid larvae, algae and detritus. Numbers of stoneflies examined are given below each column.

Table 4. Food items other than those listed in Table 3 found in guts of *Stenoperla* larvae. All animals are larvae unless stated

Food items	Number found
Hydropsyche colinica McL	13
Pycnocentrodes aureola (McL)	12
Psilochorema bidens McF	1
Hydrobiosis sp.	1
Unidentified Trichoptera	5
Unidentified trichopteran pupa	1
Chironomidae; adult	1
Unidentified dipteran adult	1
Elminthidae	2
Unidentified arthropod fragments	20
Tubificidae	1
Plant cuticle	4

Table 5. Numbers of *Deleatidium* and chironomid larvae found in guts of individual *Stenoperla* larvae

Prey species	No. of *Stenoperla* with prey species	Numbers of larvae per gut							
		1	2	3	4	5	6	7	8
Deleatidium	244	232	10	2	0	0	0	0	0
Chironomidae	69	31	15	4	6	6	2	4	1

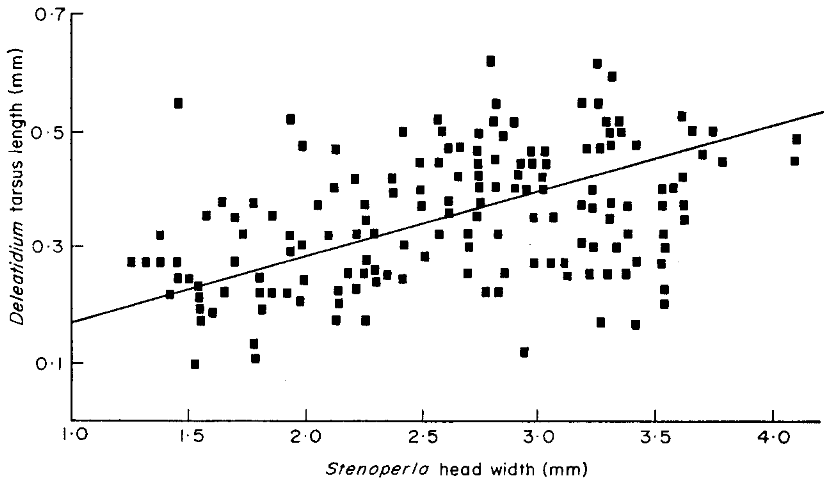

Fig. 4. Relationship between size of *Deleatidium* prey with measurable tarsi and size of *Stenoperla* larvae which had eaten them. Bartlett's 'best fit' line ($y = 0{\cdot}17 + 0{\cdot}071\ x$) is shown.

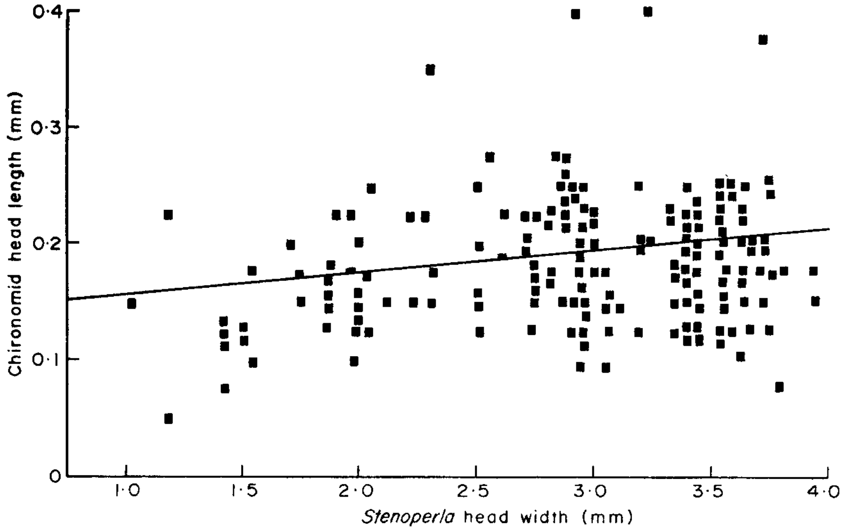

Fig. 5. Relationship between sizes of chironomid prey and *Stenoperla* larvae which had eaten them. Bartlett's 'best fit' line ($y = 0{\cdot}153+0{\cdot}013\,x$) is shown.

Figs. 4 and 5. In the case of *Deleatidium* 157 (64%) of the 244 larvae found in guts had measurable tarsi and they constitute the sample represented in the graph. Large and small stoneflies preyed upon a wide range of *Deleatidium* larvae. However, the mean size and upper size limit of prey tended to increase with increasing size of the predator. A similar, but less well defined situation was found with chironomid prey.

Results of gut analyses made in April of both years are of particular interest. In these months less animal prey was present in the guts and 72% and 55% of the stoneflies examined contained large quantities of algae. This was mainly a species of *Gomphonema* which occurred as a thick felt over much of the river bed at these times, but also included filaments of *Mougeotia* and *Oscillatoria* and diatoms belonging to the genera *Eunotia, Synedra, Amphora* and *Peronia.*

Diel feeding study

In an attempt to determine whether *Stenoperla* possessed a diel feeding rhythm, larvae were collected at intervals over a 24-h period in December 1972 and the amount and position of food in their guts was examined. In presenting the results, larvae

Table 6. Results of gut analyses carried out in December 1972 to investigate diel feeding periodicity of *Stenoperla* larvae

Time period (hours)	08.15–11.15	12.15–15.15	16.15–19.15	20.15–23.15
Larvae examined	51	23	26	32
Larvae without food	8	3	4	6
Percentage of gut length containing food ($\bar{x}\pm$SE)	36·5±3·3	40·5±3·8	36·9±4·6	31·9±4·3
Percentage of foregut containing food ($\bar{x}\pm$SE)	34·8±4·8	41·2±4·6	38·6±6·0	40·0±6·0
Hind : foregut ratio	0·48	0·38	0·35	0·27
Fore : total gut ratio	0·48	0·51	0·53	0·63

have been grouped into four, 4 hourly sets and because few animals were obtained between 24.15 and 07.15 hours no results are presented for this period.

No clear feeding rhythm was detectable (Table 6) and at all times a considerable variation in degree of gut fullness was found between larvae. In each 4-h period, 13–19% of the guts were empty and an average of 31·9–40·5% of the total gut length of all larvae contained food. Similarly, there was little difference in the mean amount of food present in the foregut at different times. As 50% of the gut length is foregut, and most of this is crop (Helson, 1934), it may be that food is stored here for considerable periods following ingestion. If this is so, then the presence of food in the foregut will not necessarily be an indication that it has been ingested recently.

Animals collected in the 4 h after dusk (Table 6, column 4) had a higher proportion of their total gut contents in the foregut, and lower hindgut : foregut fullness ratios than animals collected at other times. This could indicate that food had recently passed from the mid and hind guts and that much of the material in the foregut was recently ingested and had not had time to pass further down the digestive tract. If this interpretation is correct, then the hours around dusk should represent the period of most intensive feeding. This is a tentative conclusion based on average values, however, and it should be remembered that considerable variation was found between individual larvae.

Life history and seasonal abundance of *Deleatidium*

Total numbers of larvae collected in the six samples each month ranged from 401 to 1539. These are minimal estimates as larvae with head widths <0·44 mm (the first column in the histograms of Fig. 8) were underrepresented. Considerable variation in numbers occurred between samples taken each month (standard error of the six sample means ranged from 11–31%), but over the whole study period more larvae were found near the sides of the river than in midstream (Fig. 6). Numbers increased

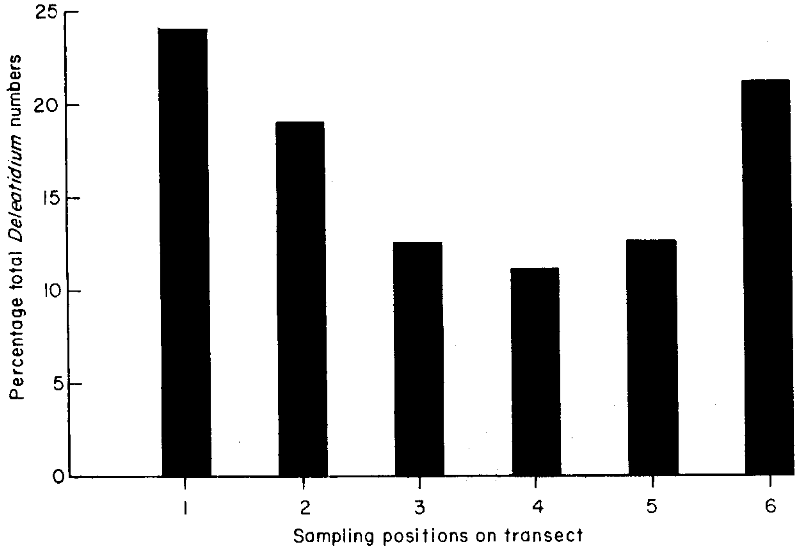

Fig. 6. Percentage of total *Deleatidium* larvae collected during the study occurring at different positions on transects across the river. Sampling positions 1 and 6 were beside the banks; 3 and 4 in midstream.

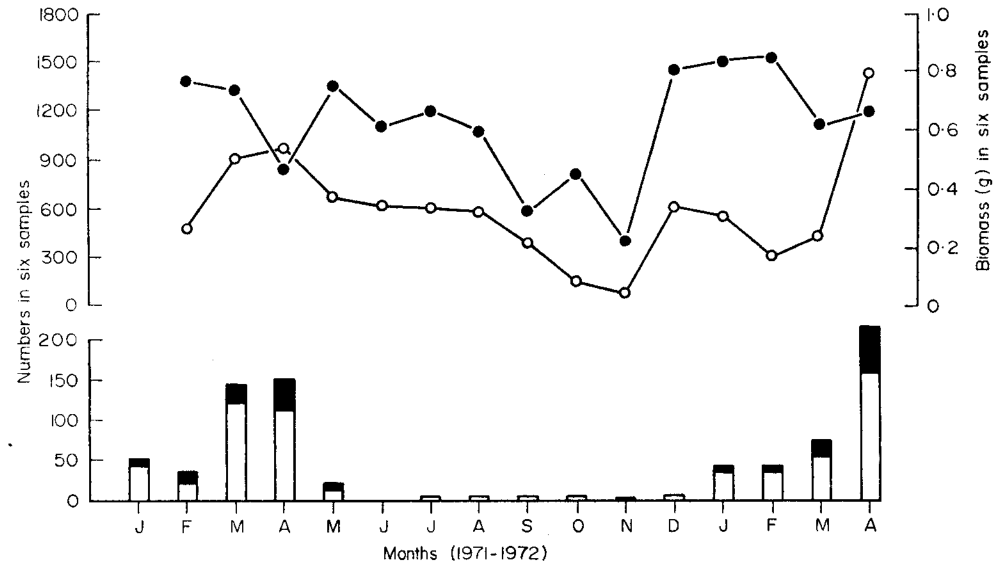

Fig. 7. Total numbers (●) and dry weights (○) of *Deleatidium* larvae taken in six Surber samples each month. Histograms show numbers of final instar larvae, and their shaded portions indicate numbers of larvae with dark wing pads. Total numbers and biomass are not given for January 1971 as small larvae were inadequately sorted from samples.

during summer when many small larvae were being recruited into the population, and highest densities were found in February of both years. Population biomass also increased over summer, and reached its maximum level in March and April when large numbers of final instar larvae were present. Biomass and density gradually declined in the following months and reached their lowest values in November (Fig. 7).

The annual cycle and pattern of growth are difficult to interpret from the monthly size distribution data, but they suggest that two overlapping generations may occur during a year; (1) a fast growing summer generation, and (2) a rather poorly defined and less synchronized winter generation. These were not clearly differentiated, however, as small larvae were entering the population throughout the year and final instar larvae were present in all months except June (Fig. 7). Larvae about to emerge could be distinguished by their dark wing pads and were found in January to May 1971, and January to April 1972. Two individuals taken in October were the only mature larvae seen outside these months.

The sex of a larva could be determined on the basis of eye dimorphism (Phillips, 1930), which first became noticeable at a head width of about 1 mm and was accompanied by the first indications of wing pad development. The sexes occurred in roughly equal proportions (53% of 788 final instar larvae collected were females), and head width measurements made on seventy-four final instar larvae of each sex indicated that, on average, females were slightly smaller than males (♀ $\bar{X}$ = 1·64 mm, range 1·48–1·88 mm; ♂ $\bar{X}$ = 1·74 mm, range 1·56–2·04 mm).

Production estimates

Larval production of both *Stenoperla* and *Deleatidium* was calculated by the method of Hamilton (1969). Potentially more accurate methods could not be employed because

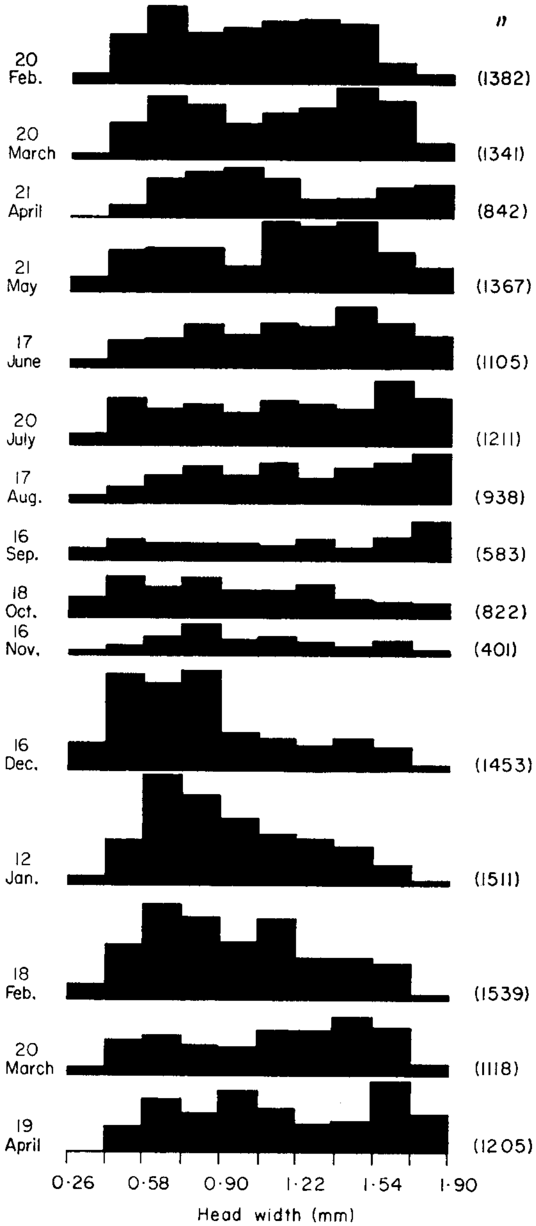

Fig. 8. Size frequency distributions of *Deleatidium* larvae taken in six Surber samples each month from February 1971 to April 1972. Sample sizes shown in brackets.

of difficulties in accurately identifying cohorts and determining patterns of growth of the two species. Production of *Stenoperla* was calculated for the year January–December 1971, the species being considered to have a 1-year life cycle. Mean annual biomass (*B*), annual production (*P*) and the annual turnover ratio (*P*/*B*) are shown in Table 7.

In calculating production of *Deleatidium*, two partly overlapping generations with

Table 7. Estimates of mean standing biomass and production of *Stenoperla* and *Deleatidium* in the Selwyn River

Species	$\bar{x}$ Biomass g/m²	Production (g/m²)/year	Turnover ratio *P/B*
Stenoperla			
January–December 1971	0·83	2·08	2·51
Deleatidium			
1971–72 summer generation	0·90	3·50	3·89
1971 winter generation	0·86	0·73	0·85
Summer + winter generations	1·22	4·23	3·47

different growth characteristics were assumed to occur each year. Production of each generation was calculated separately, and annual production was obtained by summing the two. When larvae of two generations were believed to be present in the same months (January–April, December 1971; March, April, 1972) but were not easily distinguished, an arbitrary separation was made, based on the probable growth characteristics of the larvae. The poorly synchronized winter generation declined in numbers and biomass through the year, production was low, and it exhibited a negative *P/B* ratio. By contrast, the summer generation was characterized by more rapid and more synchronized growth, production was almost five times as high, and the *P/B* ratio was almost 4 (Table 7).

Discussion

Life histories

The larval life of *Stenoperla* in the Selwyn River is probably close to 1 year, and unless eggs are present in the river bed for a long period it can be considered to be univoltine. This contrasts with Helson's (1934) conclusion that *Stenoperla* has a 2- or even 3-year life cycle, a belief based on his finding of a wide range of different-sized larvae in most of his collections. As a wide size range of larvae was also found in the Selwyn in most months because of the long egg-hatching period, this does not necessarily provide good evidence of an extended larval growth period. The Australian eustheniid, *Eustheniopsis venosa* Tillyard appears to have a 2-year life cycle (Hynes, 1964, 1970), whereas large Northern Hemisphere plecopterans have life cycles ranging from 1 year in most perlodids (Harper & Magnin, 1969; Hynes, 1970; Sheldon, 1972) to 3 or 4 years in some species of Perlidae and Pteronarcydae (Ulfstrand, 1968; Sheldon, 1969; Hynes, 1970).

The annual cycle of *Deleatidium* was difficult to interpret because although adults were emerging mainly in summer and early autumn, eggs were probably hatching throughout the year. This resulted in larvae of all sizes being present in most months. Also, larvae of different sizes were undoubtedly drifting on to the riffle, although not necessarily in proportion to their relative abundance in the river as a whole (see discussion on production estimation), and this may have affected the population size structure on the riffle, thus disguising the pattern of growth. The data obtained suggest that *Deleatidium* had two poorly differentiated generations per year, the generation growing through summer possessing the higher densities and more rapid and synchronized growth. This summer generation may have arisen from overwintering eggs as few adults appeared to be present before January. By contrast, larvae forming the main component of the winter generation probably hatched from eggs soon after these were deposited in the stream. Comparable annual cycles incorporating a single emergence period and two waves of egg hatching, resulting in a wide range of different sized larvae being present in many months, have been described for *Baetis rhodani* (Pictet) (Ulfstrand, 1968) and *Ameletus inopinatus* Eaton (Gledhill, 1959). The main difference shown by *Deleatidium* was that its egg hatching periods were less distinct, and hatching continued at low levels throughout the winter.

Feeding relationships

Helson's (1934) contentions that larvae of *Stenoperla* are carnivorous for most of their lives, and that mayfly larvae are their most important prey were confirmed by this study. Mayflies also appear to be an important food of the Australian species, *E. venosa* (Hynes, 1964), and are recognized as important foods of several Northern Hemisphere plecopterans (Minshall & Minshall, 1966; Sheldon, 1969).

In the Selwyn, *Deleatidium* larvae were the most important food items found in stonefly guts in all months, at least in terms of biomass if not always in numbers. This was probably due to their continual presence and abundance in the bottom fauna and a general paucity of alternative prey. This contrasts with the situation described by Sheldon (1969) in which *Acroneuria californica* (Banks) exhibited marked seasonal changes in prey 'selection' which were probably related to changes in abundance and availability of potential prey species.

The size range of prey eaten by stoneflies was large, although there was a tendency for larger predators to attack larger prey. This type of relationship has been described for a number of aquatic insect predators by Tachet (1965), Sheldon (1969), Winterbourn (1971), Fahy (1972) and Pritchard & Leischner (1973). The maximum size of prey attacked is not determined by its ability to be ingested whole, however, as gut content analyses and observations made in aquaria indicated that unless they were very small most prey larvae were only partially eaten. Predatory larvae of *Isoperla clio* (Newman) fed baetid nymphs acted in a similar way, often leaving behind the head and parts of the thorax (Minshall & Minshall, 1966). This type of behaviour leads to difficulties in quantifying food intake of larvae from an examination of gut contents as the few measurable fragments present cannot necessarily be equated with biomass ingested.

The switch to an algal diet by many larvae in April of both years was unexpected, and did not appear to be related to a decline in numbers of potential animal prey. Rather, it was probably a response to an increased availability of an alternative, apparently suitable food source which was only present in those months. Some species of Perlodidae (Plecoptera) and Rhyacophilidae (Trichoptera) are omnivorous (Thut, 1969; Cummins, 1973), and the trichopteran *Banksiola crotchi* Banks shows a transition from an algal to a carnivorous diet in its later instars (Winterbourn, 1971). However, I know of no other study in which a high proportion of an aquatic insect population has been shown to switch from predation to algal feeding.

Estimates of production

My production estimates are based on a riffle sampling programme and therefore assume that either all insect production occurs in the riffle area or that gains to and losses from the riffle balance each other. By taking samples from a transect across the stream it was hoped that any differences in microdistribution at different times of year, or of different-sized larvae, would be incorporated in the sampling programme. In the case of *Stenoperla*, few larvae were found in adjacent, slower-flowing stretches of stream, and as few were taken in drift samples (unpublished observations) this initial assumption appeared reasonable. The annual turnover ratio of 2·51 determined for *Stenoperla* is lower than the 3·8 obtained by Sheldon (1972) for *Skwala curvata* (Hanson) but still falls within the general range of values given by Waters (1969).

The annual turnover ratio of 3·47 calculated for *Deleatidium* was also within Waters range but several things suggest that the production estimate for this insect may be subject to considerable error.

The high intra-sample variation in numbers on each sampling day may have been a minor source of error; the loss of small individuals through the mesh of the sampler has undoubtedly led to underestimates; and between successive samplings some larval mortality would have been balanced by recruitment causing production of the population to appear lower than it was (Mann, 1969). Another factor which may have had a considerable effect on the production estimates is larval drift. *Deleatidium* larvae have a high propensity to drift (McLay, 1968) and work being carried out by R. M. Ogilvie (personal communication) in a Canterbury stream indicates that larger larvae apparently have a greater tendency to drift than smaller ones. Allen (1951) found that the average size of larvae may be larger in more rapid water, and that the highest densities of *Deleatidium* seem to occur in the quieter parts of streams such as flats and pools, rather than in riffles. This was also the case in this study where numbers were highest near the river margins. These findings suggest that some larvae, particularly larger ones, colonize riffles by drifting on to them from regions of quieter water upstream. If this was the case in the Selwyn, where the study riffle was sited immediately below an extensive flat, the riffle population could contain a higher proportion of large larvae than the overall river population. In such circumstances, riffle sampling would be expected to provide somewhat erroneous estimates of production, reflecting neither production occurring on the riffle nor in the river as a whole. Similar difficulties are likely to be encountered in studies of other stream invertebrates in which some size classes of larvae are more likely to drift than others (Waters, 1969), and in which the 'preferred' larval habitat changes during the course of the life history (Ulfstrand, 1968; McLean, 1970; Lehmkuhl & Anderson, 1972).

A further consequence of drift is that as a high proportion of larvae drifting onto a riffle may be larger than the mean size in the overall population, they should form a highly 'attractive' food source for predators like *Stenoperla*. This situation is indeed capitalized on by *Stenoperla* larvae which are found mainly in riffles and thus occupy optimal feeding stations which are not necessarily confluent with the major production sites of their prey.

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References

Allen K.R. (1951) The Horokiwi stream. A study of a trout population. *Fish Bull. N.Z.* **10**, 1–231.

Brocksen R.W., Davis G.E. & Warren C.E. (1968) Competition, food consumption, and production of sculpins and trout in laboratory stream communities. *J. Wildl. Mgmt*, **32**, 51–75.

CUMMINS K.W. (1973) Trophic relations of aquatic insects. *Ann. Rev. Entomol.* **18**, 183–206.

CUMMINS K.W. & LAUFF G.H. (1969) The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia*, **34**, 145–181.

DAVIS G.E. & WARREN C.E. (1965) Trophic relations of a sculpin in laboratory stream communities. *J. Wildl. Mgmt*, **29**, 846–871.

FAHY E. (1972) The feeding behaviour of some common lotic insect species in two streams of differing detrital content. *J. Zool., Lond.* **167**, 337–350.

GLASGOW J.P. (1936) The bionomics of *Hydropsyche colonica* McL and *H. philpotti* Till. (Trichoptera). *Proc. R. ent. Soc. Lond. A*, **11**, 122–128.

GLEDHILL T. (1959) The life history of *Ameletus inopinatus* (Siphlonuridae, Ephemeroptera). *Hydrobiologia*, **14**, 85–90.

HAMILTON A. (1940) The New Zealand dobson-fly (*Archichauliodes diversus* Walk.): life-history and bionomics. *N.Z. Jl. Sci. Technol.* **22**, 44–55.

HAMILTON A.L. (1969) On estimating annual production. *Limnol. Oceanog.* **14**, 771–782.

HARPER P. & MAGNIN E. (1969) Cycles vitaux de quelques Plécoptères des Laurentides (insectes). *Can. J. Zool.* **47**, 483–494.

HELSON G.A.H. (1934) The bionomics and anatomy of *Stenoperla prasina* (Newman). *Trans. Proc. roy. Soc. N.Z.* **64**, 214–248.

HELSON G.A.H. (1935) Hatching and early instars of *Stenoperla prasina*. *Trans. Proc. roy. Soc. N.Z.* **65**, 11–15.

HOLDSWORTH R.P. (1941) The life history and growth of *Pteronarcys proteus* Newman. *Ann. ent. Soc. Am.* **34**, 495–502.

HOPKINS C.L. (1970) Some aspects of the bionomics of fish in a brown trout nursery stream. *N.Z. Fish Res. Bull.* **4**, 38 pp.

HOWMILLER R.P. (1972) Effects of preservatives on weights of some common macrobenthic invertebrates. *Trans. Amer. Fish. Soc.* **101**, 743–746.

HYNES H.B.N. (1964) Some Australian plecopteran nymphs. *Gewäss. Abwäss.* **34/5**, 17–22.

HYNES H.B.N. (1970) *The Ecology of Running Waters.* Liverpool University Press.

ILLIES J. (1965) Phylogeny and zoogeography of the Plecoptera. *Ann. Rev. Entomol.* **10**, 117–140.

LEHMKUHL D.M. & ANDERSON N.H. (1972) Microdistribution and density as factors affecting the downstream drift of mayflies. *Ecology*, **53**, 661–667.

MANN K.H. (1969) The dynamics of aquatic ecosystems. *Adv. Ecol. Res.* **6**, 1–81.

MCDOWALL R.M. (1965) Studies on the biology of the red-finned bully *Gobiomorphus huttoni* (Ogilby). III. Food studies. *Trans. R. Soc. N.Z.* (*Zool.*) **5**, 177–196.

MCLAY C.L. (1968) A study of drift in the Kakanui River, New Zealand. *Aust. J. mar. Freshwat. Res.* **19**, 139–149.

MCLEAN J.A. (1970) Studies on the larva of *Oniscigaster wakefieldi* (Ephemeroptera: Siphlonuridae) in Waitakere Stream, Auckland. *N.Z. Jl. mar. Freshwat. Res.* **4**, 36–45.

MINSHALL G.W. & MINSHALL J.N. (1966) Notes on the life history and ecology of *Isoperla clio* (Newman) and *Isogenus decisus* Walker (Plecoptera : Perlodidae). *Am. Midl. Nat.* **76**, 340–350.

MUNDIE J.H. (1971) Sampling benthos and substrate materials, down to 50 microns in size, in shallow streams. *J. Fish. Res. Bd Canada*, **28**, 849–860.

PHILLIPS J.S. (1930) A revision of New Zealand Ephemeroptera. Part 2. *Trans. Proc. N.Z. Inst.* **61**, 335–390.

PRITCHARD G. & LEISCHNER T.G. (1973) The life history and feeding habits of *Sialis cornuta* Ross in a series of abandoned beaver ponds (Insecta; Megaloptera). *Can. J. Zool.* **51**, 121–131.

RIEK E.F. (1970) Plecoptera. In: *The Insects of Australia.* Ed by I. M. Mackerras, pp. 314–322. Melbourne University Press.

SHELDON A.L. (1969) Size relationships of *Acroneuria californica* (Perlidae, Plecoptera) and its prey. *Hydrobiologia*, **34**, 85–94.

SHELDON A.L. (1972) Comparative ecology of *Arcynopteryx* and *Diura* (Plecoptera) in a California stream. *Arch. Hydrobiol.* **69**, 521–546.

TACHET H. (1965) Influence du stade larvaire et de la saison sur l'alimentation des larves de *Polycentropus* (Trichoptère) dans des conditions naturelles. *Ann. Soc. Ent. Fr.*, (*N.S.*) **1**, 635–640.

THUT R.N. (1969) Feeding habits of larvae of seven *Rhyacophila* (Trichoptera : Rhyacophilidae) species with notes on other life-history features. *Ann. ent. Soc. Am.* **62**, 894–898.

ULFSTRAND S. (1968) Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). *Oikos*, **19**, 167–190.

Waters T.F. (1969) The turnover ratio in production ecology of freshwater invertebrates. *Amer. Nat.* **103**, 173–185.

Winterbourn M.J. (1966) Studies on New Zealand stoneflies 2. The ecology and life history of *Zelandoperla maculata* (Hare) and *Aucklandobius trivacuatus* (Tillyard)-(Gripopterygidae). *N.Z. Jl. Sci.* **9**, 312–323.

Winterbourn M.J. (1971) An ecological study of *Banksiola crotchi* Banks (Trichoptera, Phryganeidae) in Marion Lake, British Columbia. *Can. J. Zool.* **49**, 637–645.

Wisely B. (1961) Studies on Ephemeroptera 1. *Coloburiscus humeralis* (Walker); early life history and nymph. *Trans. R. Soc. N.Z., Zool.* **1**, 249–257.

Wisely B. (1962) Studies on Ephemeroptera 2. *Coloburiscus humeralis* (Walker); ecology and distribution of the nymphs. *Trans. R. Soc. N.Z., Zool.* **2**, 209–220.