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The feeding relationships of two invertebrate predators in a New Zealand river

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Summary

The size frequency distributions and foods of the larvae of Archichauliodes diversus (Megaloptera: Corydalidae) and Stenoperla prasina (Plecoptera: Eustheniidae) were studied for a year in the Glentui River, South Island, New Zealand. These two species are the largest invertebrate predators inhabiting streams and rivers in New Zealand, where they are the only carnivorous members of their respective orders. Both species occupied the same habitat with A. diversus being slightly more abundant in most months. Many small larvae occurred within the sediments of the stream bed, whereas more larger larvae were found on stones lying on the surface. A wide size range of larvae was present throughout the year and the median size (in terms of head width) of both species was similar in most months. Larval growth could not be determined from field data and the life cycles of both species can be described as non-seasonal. Quantitative sampling in 5 months provided estimates of population densities. These were maximal in December when values of $136/m^2$ *for A. diversus and* $114/m^2$ *for S. prasina were obtained.*

Larval Chironomidae and mayflies of the genus Deleatidium were the most frequently taken prey of both predators in all months, and no strong relationship between size or species of predator and size of prey was found. Caseless trichopteran larvae formed a less important component of the diets of both species and detritus was ingested by some individuals. No instances of cannibalism and only one example of cross-predation by each predator was seen. Diel sampling in November showed that large Deleatidium larvae were relatively more abundant in the guts of insect predators and in nocturnal drift samples than in the benthos. This suggests that their greater activity at night may increase their susceptibility to predation by nocturnal feeders.

No clear ecological segregation of the two species with respect to habitat or prey utilization was found and there was no obvious interspecific competition for food, which appeared to be abundant at all times. Finally, the prevalence of non-seasonal life cycles in New Zealand aquatic insects is discussed in relation to the low degree of speciation in several groups.

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Introduction

Larvae of *Archichauliodes diversus* (Walker) (Megaloptera: Corydalidae) and *Stenoperla prasina* (Newman) (Plecoptera: Eustheniidae) are the largest invertebrate predators inhabiting New Zealand streams. They are the only aquatic carnivores in their respective orders in New Zealand, both being widely distributed within the country and often occurring together. Although monotypic genera in New Zealand, four species of *Stenoperla* and nine species of *Archichauliodes* are known from Australia while representatives of the latter genus also occur in Chile (Riek, 1970). The trophic relationships of *S. prasina* have been studied in a river from which megalopterans were absent (Winterbourn, 1974), but feeding of *A. diversus* has not been examined in detail.

Most studies on the feeding relationships of aquatic insect predators have been largely descriptive, listing prey species found by gut or faecal analyses, or have considered such questions as prey selection and prey availability (Cummins, 1973; Bay, 1974). The important theoretical concepts of ecological segregation and competition between species have been discussed to some extent by Grant & Mackay (1964) and Sheldon (1972) but few attempts have been made to examine them directly. Where predators coexist, differences in feeding, perhaps associated with differences in life history patterns or spatial distribution might be expected to occur as a mechanism for avoiding competition. Such differences have been shown for coexisting species of *Rhyacophila* (Trichoptera) by Thut (1969), and Perlodidae (Plecoptera) by Sheldon (1972), but in other cases (e.g. Fahy, 1972) little evidence for ecological segregation of potential competitors has been found.

In the present study, the size frequency distributions and foods of *A. diversus* and *S. prasina* larvae occurring together on a riffle in a New Zealand river were compared over a 13-month period, and on the basis of this the questions of interspecific competition and ecological segregation are discussed.

Study area

Fieldwork was carried out in the Glentui River, 56 km north of Christchurch in the South Island of New Zealand. The sampling site was a riffle about 50 m long and 3–4 m wide, lying at the bottom of a steep, V-shaped valley whose sides were covered with mountain beech, *Nothofagus solandri* (Hook). The river bed consisted of gravel and silt 40–50 mm deep lying on a base of compacted soil. Large stones 50–350 m across were scattered above the gravel in many places. No macrophytes were present. The Glentui is subject to heavy flooding after prolonged periods of rainfall such as occurred in August and November 1973 during this study. At these times, water velocities sometimes exceeded 3 m s^{-1} and considerable movement of bed material occurred. Mean flow rates in the middle of the riffle area under normal conditions were 0·4–0·5 m s^{-1}. Water temperatures on sampling days ranged from 3·5°C in July to 14·5°C in February.

In addition to the present work, several other biological studies are being carried out in the Glentui River. These include a recently completed investigation of the biology of *Galaxias vulgaris* Stokell and other fish (Cadwallader, 1973), and ongoing studies of population processes, production and micro-distribution by R. M. Ogilvie and the present authors.

Methods

Bottom samples were taken at about monthly intervals from February 1973 to February 1974. Animals were collected into 0·5- and 1·0-mm mesh nets by the foot-kick method and by turning over and washing stones throughout the study area. Sampling was continued until sufficient specimens were thought to have been taken. This number (thirty to eighty of each species in most months (Table 1)) represented a compromise between the number whose gut contents could be analysed in the time available and the number which would provide a reasonable indication of population size structure. Samples were difficult to take when the river was in flood, and at such times collections could be made only at the river margins. All animals were preserved in 10% formalin immediately after collection.

Because of the uneven nature of the stream bed in the study area, the irregular distribution of larvae and their relatively low numbers, no attempt was made to obtain data on insect densities as part of the monthly sampling programme. Some information on the abundance of *A. diversus*, *S. prasina* and their prey was obtained in December 1973 and February 1974, however, using a sampler of the type described by Waters & Knapp (1961) (area sampled 0·05 m^{2}; pore size 0·35 mm). Three sampling units were taken on each occasion but as they could be taken only where stones were small enough to fit within the sampler frame, they were not necessarily representative of the riffle as a whole. Numbers of larvae on stones lying on the upper surface of the river bed were also determined on the same days by collecting the fauna from individual stones (forty in November, twenty-four in February) in the manner described by Ulfstrand (1967). Densities were then calculated in terms

Table 1. Numbers of larvae of *A. diversus* and *S. prasina* taken from the Glentui River each month from February 1973 to February 1974. Gut contents of all larvae were examined except those collected in February 1974

	Months													Totals
	F	M	A	M	J	J	A	S	O	N	D	J	F	
A. diversus	38	46	122	86	51	76	43	43	67	57	72	93	96	1531
S. prasina	10	14	89	66	39	69	37	63	67	34	47	54	52	890
% *A. diversus*	79	77	58	57	57	53	54	41	50	63	61	63	65	58

of standard areas (mean length × mean width) of the under-surfaces of the stones sampled. The main aim of this stone-sampling programme was to examine the microdistribution of ephemeropteran larvae and the results of that study will be presented elsewhere along with further details of the methodology employed. The most reliable information on abundance of the two predators was obtained in 4 months from samples taken by R. M. Ogilvie in a straight, 200-m section of the river, upstream of and adjoining the main study area. In this section, substrate and flow conditions were more uniform and as few large stones occurred, better population estimates could be made with the Waters and Knapp sampler.

Drift sampling was carried out in the middle of the study area in conjunction with the November microdistribution study. Samples were taken every 3 h over 24 h with a rectangular mouthed drift net (area 0·045 m^2; pore size 0·35 mm), held 20 mm above the stream bed by a wooden rail.

Gut analyses

The gut contents of 1373 larvae (589 *S. prasina* and 784 *A. diversus*) were examined during the study. A gut was removed from a larva by pulling off the head to which the gut remained attached. It was placed on a microscope slide, its contents teased out, and mounted in lactophenol-PVA containing the stain Lignin Pink. Head widths of all predators and prey animals were measured with a linear eyepiece graticule at ×40 except for the ephemeropteran *Deleatidium* when tarsal lengths were measured. These provide a useful measure of body size as they are the same length on all legs (with the exception of the foretarsi of male larvae which are longer, but easily recognized and so avoided), they normally remain intact within a predator's gut and there are six (four in males) chances that one will be found.

Results

Size frequency distribution

Numbers of *A. diversus* and *S. prasina* larvae collected from the riffle each month are given in Table 1. In most months slightly more *A. diversus* than *S. prasina* were taken and over the 13-month period they accounted for 58·1 % of the larvae collected. Monthly size frequency distributions of both species are shown in Fig. 1 in which larvae are grouped into arbitrarily chosen 0·4-mm size classes as individual instars could not be detected. Both species possessed a wide size range throughout the year but their average sizes were very similar each month as indicated by median head width measurements (Fig. 5). Head width is a useful indicator of size in predation studies such as this, as it is strongly correlated with mouth 'gape' which determines the maximum size of ingestible prey. Most small larvae of both species were found in spring and early summer, but some also occurred in all other months. Life history patterns could not be interpreted clearly from the size frequency data, and they can be defined as non-seasonal, following Hynes (1970). In the Selwyn River, 55 km south-east of the Glentui, *S. prasina* appears to have a 1-year larval growth period (Winterbourn, 1974) and there is some suggestion that this may also be the case in the Glentui. *A. diversus* is thought to have a larval life of greater than 1 year (Hamilton, 1940) as larvae of various sizes are present at all times but only one emergence period occurs. A similar situation is described by Riek (1970)

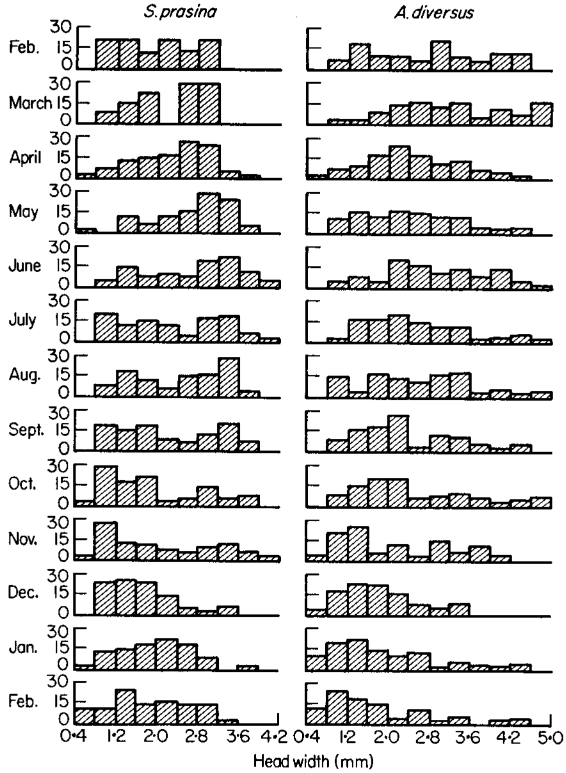

Fig. 1. Size frequency distributions of *S. prasina* and *A. diversus* larvae from February 1973 to February 1974. Units given on the ordinates are percentages.

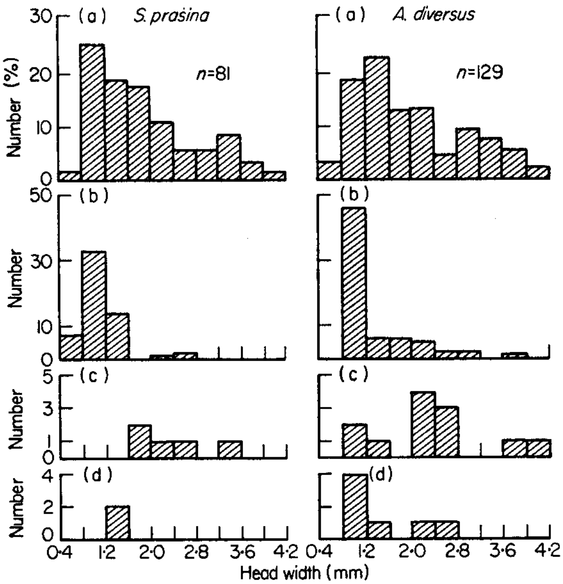

Fig. 2. Comparison of the size frequency distributions of *S. prasina* and *A. diversus* larvae taken in the Glentui River by different methods in November–December 1973. (a) Brushing stones and foot kicking in main study area; (b) Waters & Knapp samples from upstream area; (c) Ulfstrand samples from main study area; (d) Waters & Knapp samples from main study area.

for an unidentified Australian species of *Archichauliodes* whose rate of development is not known but which probably has a life cycle of more than 2 years.

When the size frequency distributions of larvae in samples from the main study area are compared with those taken in Waters & Knapp samples from more uniform, finer sediments upstream some interesting differences are found (Fig. 2). In all months (November–December results only shown), the upstream samples contained higher proportions of very small larvae of both species and few large larvae were taken. This is probably a result of the different sampling methods used and differences in the substrates examined. When collecting with the Waters & Knapp sampler, finer sediments were disturbed to a greater depth (up to 15 mm), whereas collections made in the main study area were predominantly from larger, surface stones. This suggests that many small larvae live among finer sediments, whereas a high proportion of larger larvae occupy the undersurfaces of larger stones (at least during the day). This contention is borne out further by the results of individual stone, and Waters & Knapp sampling carried out in the main riffle in November, even though only small numbers of animals were obtained (Fig. 2). These subtle habitat differences which were not taken into account by the regular monthly sampling programme, also contribute to the problem of defining life history patterns.

Abundance of larvae

Density estimates obtained for *S. prasina* and *A. diversus* in two sections of the Glentui River on several occasions during 1973–74 are shown in Table 2. Standard errors calculated for Waters & Knapp samples containing seven or more sampling units ranged from 16 to 55% of the means indicating that the distribution of larvae was highly contagious in relation to the sampling units employed. Because of this, the mean values shown are fairly broad approximations of the true densities. Higher numbers of both species were found in the upstream section than in the main study area, with maximum densities (*S. prasina* 114/m^2; *A. diversus* 136/m^2) occurring in December. This compares with a maximum density of 143/m^2 for *S. prasina* (*A. diversus* was absent) in the Selwyn River in December 1971 (Winterbourn, 1974). The lower numbers obtained

Table 2. Numbers of larvae in quantitative bottom samples taken from the main study area and a more uniform stretch of river upstream. Samples were taken with a Waters & Knapp sampler (W & K) or by Ulfstrand's individual stone method (Ulfstrand)

Date	Sampling method	Number of sampling units	Location	Number of larvae/m^2			Predator: *Deleatidium* ratio (%)
				S. prasina	*A. diversus*	*Deleatidium*	
1 July 1973	W & K	10	Upstream	56	20	4320	1·8
1 Aug. 1973	W & K	7	Upstream	32	14	2800	1·6
30 Nov. 1973	W & K	12	Upstream	52	92	2480	4·8
30 Nov. 1973	W & K	3	Study area	7	60	3500	1·9
27 Nov. 1973	Ulfstrand	40	Study area	6	12	3062	0·6
24 Dec. 1973	W & K	10	Upstream	114	136	5440	4·6
20 Feb. 1974	W & K	3	Study area	46	40	2906	3·0
20 Feb. 1974	Ulfstrand	24	Study area	15	21	1698	2·1

with Ulfstrand's (1967) individual stone sampling method provide further evidence that the insects are not confined to stones lying on the surface of the bed.

Food

Larvae of both species take a wide range of food items (Table 3). *Deleatidium* larvae, possibly belonging to several species which could not be told apart, were the most common prey of *A. diversus* (46%) and also formed a high proportion of the food items in *S. prasina* guts (38%). Larval Chironomidae were numerically the most common prey of *S. prasina*. They were smaller than most of the mayfly larvae taken and often occurred in higher numbers in the guts of individual predators than did *Deleatidium* (Table 4). Other animal prey formed only a small percentage of the total food items of both predators; 12% in *A. diversus* and less than 10% in *S. prasina*. Trichopteran larvae, particularly caseless species of Rhyacophilidae, Hydropsychidae and Philopotamidae formed the largest group of other prey. Larval Elmidae and cased caddis larvae, principally Sericostomatidae, although numerically important components of the benthos, were rarely taken by either predator. In this respect *S. prasina* and *A. diversus* resemble some other carnivorous plecopteran and megalopteran larvae whose food habits have been studied in detail (Mackereth, 1957; Stewart, Friday & Rhame, 1973). Although gut contents of 1373 insects were examined, no instances of cross-predation between *A. diversus* and *S. prasina* were found. This was unexpected as the two predators are found in the same habitat and sometimes even on the same stone, and Hamilton (1940) has stated that *A. diversus* larvae, 'will grab and masticate with their powerful jaws any insect that crosses their path'. By contrast, one case of cannibalism, by an individual of each species was found.

Table 3. Food items found in the guts of *A. diversus* and *S. prasina* larvae. Figures given are percentages of all food items found. Animal prey are larvae unless otherwise stated. Presence of detritus in a gut is considered as a single food item

Food items	*A. diversus*	*S. prasina*
EPHEMEROPTERA		
Deleatidium spp.	46·2	38·4
Nesamaletus ornatus	—	0·2
Coloburiscus humeralis	0·8	0·6
PLECOPTERA		
Stenoperla prasina	—	0·1
Aucklandobius trivacuatus	0·3	0·6
Zelandoperla maculata	—	0·1
TRICHOPTERA		
Pycnocentrodes aureola	1·9	0·5
Olinga feredayi	0·2	—
Hydropsyche colonica	3·7	1·0
Hudsonema amabilis	—	0·1
Hydrobiosis clavigera	0·6	0·1
Psilochorema sp.	0·6	0·2
Dolophilodes stenocerca	0·5	—
Unidentified Rhyacophilidae	2·5	1·6
Unidentified fragments	0·8	0·3
Pupae	0·6	—
COLEOPTERA		
Elmidae	1·1	0·2
MEGALOPTERA		
Archichauliodes diversus	0·2	—
DIPTERA		
Chironomidae	16·1	47·4
Chironomid pupae	—	1·1
Unidentified larvae and adults	1·0	1·2
ACARINA	1·7	—
DETRITUS	18·5	4·3
UNIDENTIFIED MATERIAL	2·5	2·2

— = not found.

Seasonal variations in occurrence of the three main foods are shown in Fig. 3. Both species fed throughout the year although in every month some larvae had empty guts. *Deleatidium* and chironomid larvae were abundant in the river throughout the year and were taken by both predators in all months. No clear seasonal changes in diet were found. Similarly, detritus was ingested by both species in most months, with slightly more animals tending to contain detritus in winter than summer. Differences in diet in relation to size of predators are shown in Table 5. *A. diversus* of all sizes ate similar foods although those in the smallest class ate slightly more detritus and fewer mayfly larvae, and those in the three largest

Table 4. Numbers of *Deleatidium* and chironomid larvae found in guts of *A. diversus* and *S. prasina*

Predator	Prey species	Number of predators with prey species	Number of larvae per gut				
			1	2	3	4	>4
S. prasina	*Deleatidium*	281	213	52	12	4	—
	Chironomidae	118	59	20	9	5	25
A. diversus	*Deleatidium*	239	198	36	5	—	—
	Chironomidae	64	45	11	4	—	4

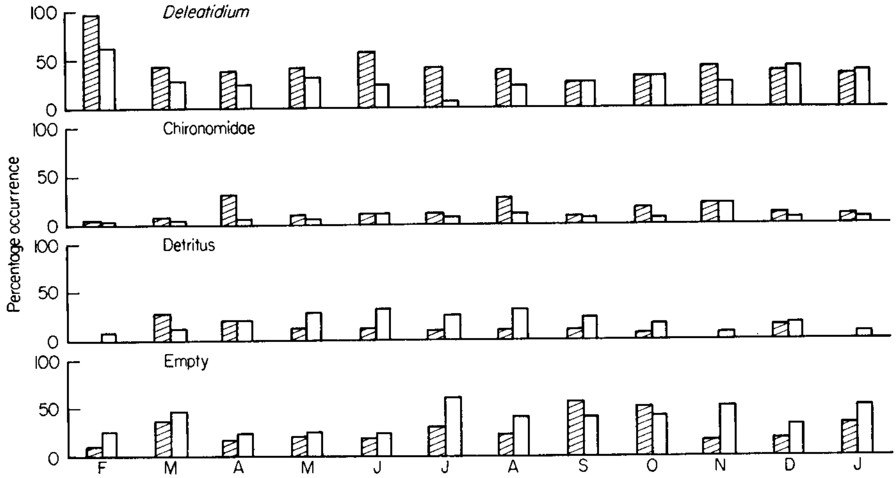

Fig. 3. Percentage of *S. prasina* (hatched columns) and *A. diversus* (open columns) larvae dissected each month containing fragments of *Deleatidium* larvae, chironomid larvae, detritus and empty.

classes took higher numbers of trichopteran prey. No marked differences in gut contents were found between *S. prasina* of different sizes, although as larvae grew larger, more *Deleatidium* but fewer Chironomidae were eaten. Detritus was found most frequently in the two smaller size classes, but small numbers of caddis larvae were taken by larvae of all sizes. Of the *Deleatidium* found in the guts of *A. diversus*, 76% had measurable tarsi compared with 80% of those in *S. prasina*. Prey within the same size range were taken by both species (Fig. 4) although slightly more large larvae (tarsal length >0·5 mm) were eaten by *A. diversus* whereas more small ones (tarsal length <0·1 mm) were taken by *S. prasina*. A general tendency was found for larger individuals of both species to take a wider size range of *Deleatidium* prey than smaller predators, and for the average size of prey to increase slightly with an increase in predator size. No such trends were found for chironomid prey. The median size of mayfly prey eaten by the two species each month varied little during the year or between predators (Fig. 5), although in most months the median size of prey eaten by *A. diversus* was a little greater than that taken by *S. prasina*. Median sizes of the two predators in terms of head width were also very similar each month and a reduction in median prey size corresponding to a decline in median predator size could be seen at the end of the year.

The relationship between size of *Deleatidium* larvae

Table 5. Percentage occurrence of different food items in the guts of five size classes of *A. diversus* and *S. prasina* larvae. All monthly samples are combined

Size classes (head width mm)	No. of larvae	Percentage of larvae containing six foods					
		Deleatidium	Chironomidae	Detritus	Caseless caddis	Cased caddis	Other
A. diversus							
<1·2	93	32·1	14·1	32·1	5·4	—	16·4
1·3–1·9	203	45·0	10·0	20·0	10·7	—	14·2
2·0–2·6	199	45·0	17·2	21·8	9·0	2·1	4·9
2·7–3·3	140	43·0	11·5	27·6	7·5	4·1	6·2
>3·3	158	51·0	7·2	17·6	10·5	3·2	9·6
S. prasina							
<1·2	88	33·0	37·1	10·2	5·8	—	13·9
1·3–1·9	153	51·3	21·5	17·3	3·8	—	6·4
2·0–2·6	120	52·7	22·5	5·0	3·4	0·9	15·6
2·7–3·3	155	58·0	18·5	3·1	5·7	1·5	11·8
>3·3	73	66·2	16·5	8·3	3·9	1·3	3·9

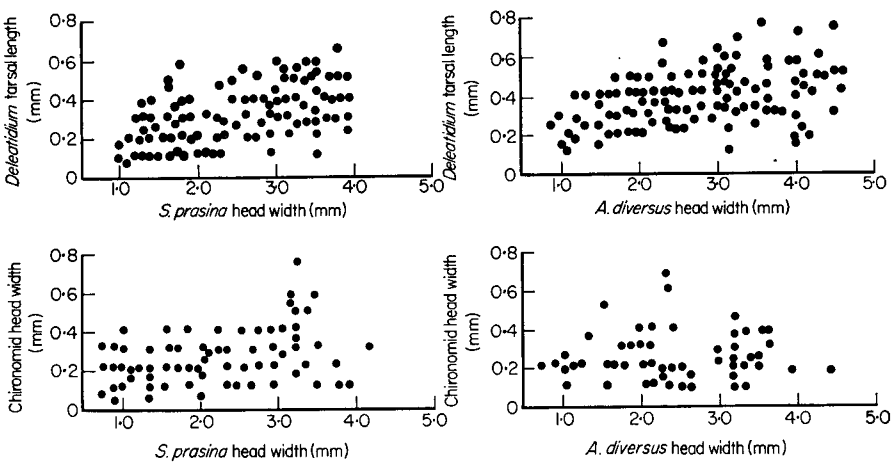

Fig. 4. Scatter diagrams showing the sizes of *Deleatidium* and chironomid prey and the *S. prasina* and *A. diversus* larvae which had eaten them.

in the benthos, drift and guts of *S. prasina* and *A. diversus* was examined in November–December 1973 (Fig. 6). The size frequency distribution of the mayfly population was determined by measuring head capsule widths of 771 larvae occurring on twenty stones from two transects taken across the study riffle on 27 November. The regular November and December collections provided information on sizes of prey eaten. Whereas the river population was dominated by small individuals, the gut contents of both predators, especially *A. diversus* contained a disproportionate number of middle-sized and large larvae. During the day, few larvae were drifting and most of these were small individuals. However, at night many more larvae occurred in the drift and they included individuals of all sizes, middle- and large-sized ones being most abundant. It is probable that *S. prasina* and *A. diversus* are primarily visual and nocturnal predators, and it is likely that drift sampling provides a reasonable measure of the general activity of a population (Elliott, 1967). Therefore, it is possible that the increased activity of larger mayfly nymphs at night, in proportions greater than their relative abundance in the benthos, makes them more likely to be preyed upon by insect predators.

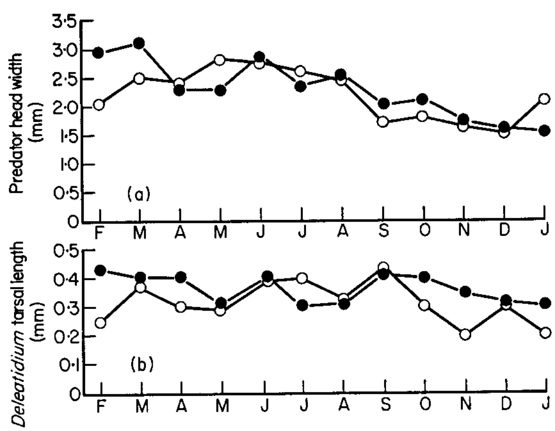

Fig. 5. (a) Median head widths of *A. diversus* (●) and *S. prasina* (○) larvae each month from February 1973 to January 1974. (b) Median tarsal lengths of *Deleatidium* larvae from the guts of *A. diversus* (●) and *S. prasina* (○).

Discussion

S. prasina and *A. diversus* are the largest benthic invertebrates in the Glentui River. Individuals of all sizes are carnivorous although detritus is also ingested by some larvae. The foods of the two species were very similar, and they did not specialize on different kinds or sizes of prey. Larvae belonging to the ephemeropteran genus *Deleatidium*, and species of Chironomidae were the main food items throughout the year, together making up 89% of the animal prey items ingested by *S. prasina* and 76% of those taken by *A. diversus*. This is similar to the situation found in the Selwyn River where these two groups comprised 84% of the prey items taken by larvae of *S. prasina* (Winterbourn, 1974). Measurements of mayfly prey showed that a wide size range of larvae were being eaten each month and that the median size of *Deleatidium* prey varied little from month to month.

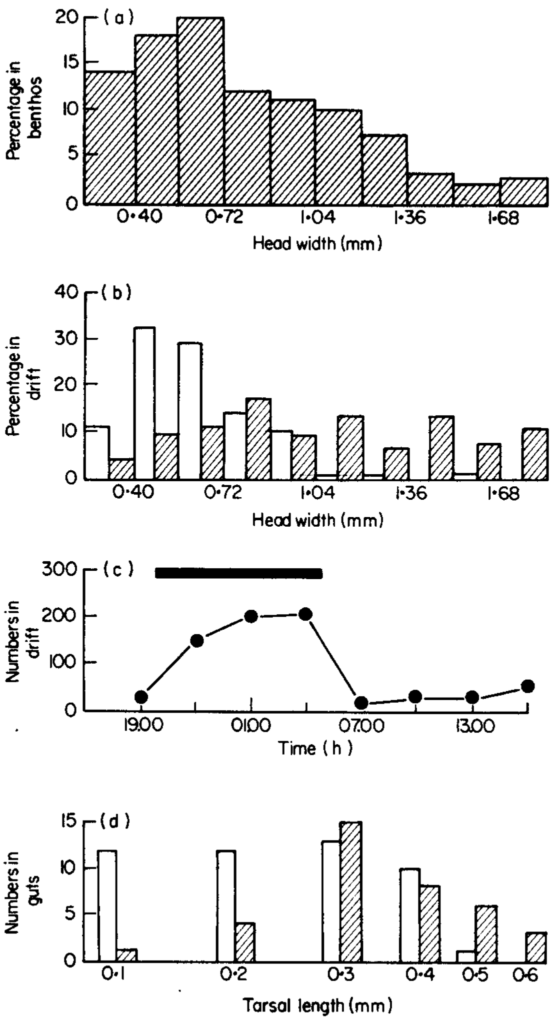

Fig. 6. A comparison between the size frequency distributions of *Deleatidium* larvae. (a) In the benthos (15 November 1973); (b) in the drift (30 November–1 December 1973); (d) in the guts of *A. diversus* (hatched columns) and *S. prasina* (open columns) in November and December 1973. In (b) the open columns show background (07.00–16.00 hours) drift, and hatched columns the period of maximum drift (01.00–04.00 hours). Numbers of *Deleatidium* taken in 3-h drift samples are shown in (c) the horizontal bar indicating the period between sunset and sunrise. In graph (d) tarsal lengths have been grouped to the nearest mm and plotted so as to allow a direct comparison with headwidth data in (a) and (b).

Deleatidium larvae also form a substantial part of the diets of three fish, *G. vulgaris*, *Gobiomorphus breviceps* (Stokell) and *Salmo trutta* L. in the Glentui and are taken frequently by the eels *Anguilla australis schmidtii* Phillips and *A. dieffenbachii* Gray (Cadwallader, 1973). They are also eaten by several species of Rhyacophilidae (Trichoptera) although dipteran larvae, particularly Chironomidae are their major prey (Winterbourn, unpublished). *Deleatidium* is clearly the most heavily preyed upon member of the bottom fauna which is not entirely unexpected, as it is also the most abundant taxon in the bottom fauna, and large numbers of larvae of a wide range of sizes are maintained throughout the year.

Few detailed studies of the trophic relations of other larval Corydalidae have been made although it is generally recognized that they are actively predacious and take a variety of primarily insect prey (Gurney & Parfin, 1959). The North American species *C. cornutus* has been studied by Stewart *et al.* (1973) who found that like *A. diversus*, it had a diverse diet which changed little with increasing larval size, and was dominated by species present in the environment in large numbers and with high availability.

S. prasina like many carnivorous stoneflies, feeds to a large extent on ephemeropteran and dipteran larvae and like *Perlodes microcephala* (Pictet) (= *Perlodes mortoni* Klapalek) a European stonefly of comparable size, the diets of different sized larvae are generally similar (Jones, 1950). Another European species, *Perla bipunctata* Pictet (= *Perla carlukiana* Klapalek) also resembles *S. prasina* in taking the same prey species (principally *Baetis* spp.) in most months of the year (Mackereth, 1957), although whether different sized prey were taken in different months was not examined. These findings contrast with those described by Sheldon (1969) for the North American stonefly, *Acroneuria californica* (Banks) in which a wide size range of larvae was present each month. He found a strong relationship between sizes of predators and their ephemeropteran prey, although weaker relationships existed for dipteran and trichopteran prey. Median prey sizes showed considerable differences from month to month, and in general the largest predators ate caddisfly larvae in all months, intermediate-sized predators ate mayfly larvae whereas small stoneflies ate mainly Diptera.

In the only other comparison between a corydalid and a carnivorous plecopteran living together in a river, Vaught & Stewart (1974) found that the diets of both species overlapped considerably in 2 of the 3 months compared. At these times larval and pupal Chironomidae and *Simulium* were important prey, but in a third month there was 'a major shift in overall diet' of the corydalid to include large numbers of *Hydropsyche*. Unfortunately, this study was made only in spring and prey size was not considered so further comparisons with our results cannot usefully be made.

The life cycles of *A. diversus* and *S. prasina* were non-seasonal in the Glentui River, larvae of all sizes being present in all months. Hynes (1961) noted that this was the case for a disproportionate number of carnivores, but it also seems typical of many aquatic insects in New Zealand which are not carnivorous and are relatively small, including species of Ephemeroptera, Plecoptera, Trichoptera and Coleoptera (Tan, 1961; Norrie, 1969; Michaelis, 1974; Winterbourn, 1974 and unpublished). Notable exceptions are some species of the plecopteran family Gripopterygidae (Winterbourn, 1966 and unpublished). This contrasts with the situation outlined in numerous Northern Hemisphere studies in which many aquatic insects have been found to possess well-synchronized, seasonal cycles (Hynes, 1970). The unusualness of having a wide range of different sized larvae present at one time has been emphasized by Harper (1973) who has described it as an 'interesting peculiarity'. Hynes (1961) and Harper (1973) have suggested that the presence of a wide range of larvae by a predator at any one time would lessen intraspecific competition, assuming that prey organisms change with size of the predator. Similarly, it should be advantageous for species with well-synchronized life cycles to have growth patterns which are slightly out of phase (again, if prey organisms change with size of the predator). Such temporal separation has been described for perlodid species by Harper (1973). In the case of *A. diversus* and *S. prasina*, larvae of all sizes feed on similar prey (size and kind) and the simultaneous presence of a wide range of different sized larvae would probably do little to reduce the likelihood of inter- or intraspecific competition for food if such competition exists. Kawanabe (1959) and Hynes (1970) have argued that similarity or near identity of diet between two species in the same habitat indicates that they are not competing for food. Rather they believe that a change in diet by one species caused by the presence of the other would indicate such competition. The close similarity of the diets of *A. diversus* and *S. prasina* in the Glentui and between larvae of *S. prasina* in the Glentui and Selwyn Rivers, from which *A. diversus* was absent (Winterbourn, 1974) suggests, therefore, that the two species were not competing for food. The presence of abundant *Deleatidium* and chironomid larvae of all sizes in the benthos in all months (Table 2 and R. M. Ogilvie personal communication) also suggests that food is never a scarce resource as does the very low incidence of cannibalism and the lack of cross predation between the two predators. As well as recruitment of young larvae from eggs hatching over extended periods, drift may well provide an important mechanism contributing to the maintenance of high numbers of prey species in the predators' feeding stations. Large numbers of drifting *Deleatidium* larvae were taken in November during the present study, and regular monthly sampling by R. M. Ogilvie just above the study area has shown that high *Deleatidium* drift densities are found throughout the year.

Finally, it is interesting to note that *S. prasina* and *A. diversus* are the sole representatives of their respective families in New Zealand and are also the only carnivorous plecopteran and megalopteran inhabiting New Zealand streams and rivers. A low degree of speciation is characteristic of many of the aquatic insect orders in New Zealand (Dumbleton, 1970) and one consequence of this is that some species could be expected to occupy broader 'ecological niches' than many of their better known Northern Hemisphere counterparts. Hynes (1970) has speculated that in the tropics, reproduction and growth may be continuous so that all life history stages would be present at all times. As it seems usual for the growth and emergence periods of co-occurring, closely allied species to be separated in time, he has suggested, therefore that, 'in any one section of a tropical stream each genus or life-form would have a greater tendency to be represented by only one species'. It seems possible that this type of situation is being approached in New Zealand, which although hardly tropical, has a generally mild climate and a high proportion of aquatic insects, not only carnivores, with non-seasonal or slow-seasonal life cycles and long emergence periods.

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