

Food resources and ingestion patterns of insects along a West Coast, South Island, river system*

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Abstract Food utilisation by benthic insect larvae at 6 sites along a West Coast, South Island river system (Devils Creek and the Inangahua River) was studied by gut content and stable carbon isotope analyses. At forested and open sites the dominant materials ingested by all species of Ephemeroptera, Plecoptera, and Trichoptera examined were fine detrital particles in the 0.45–75 µm size range. Diatoms and filamentous algae were eaten in varying amounts by some species. Larvae of *Deleatidium* (Ephemeroptera) and Chironomidae were the numerically dominant prey of the stonefly, *Stenoperla prasina* at all sites. Stable carbon analyses indicated that most species were dependent largely on carbon of terrestrial origin at forested sites, whereas autochthonous material was used increasingly further down Devils Creek. However, in the large, open Inangahua River ¹³C/¹²C ratios of insects

were similar to those found in the forested tributaries and indicated a return to allochthonous dependence by the fauna. Although algae appeared to be ingested sparingly by stone-surface browsers at forested sites, some such as *Deleatidium* had ¹³C/¹²C ratios indicating the incorporation of substantial autochthonous carbon. To explain this it is suggested that heterotrophic organisms within stone-surface organic layers use algal exudates as a major source of energy, and that they and their products (e.g., slimes) are subsequently ingested and assimilated by organic layer feeders.

Keywords allochthonous; autochthonous; detritus; algae; stable carbon isotopes; streams; aquatic insects; Ephemeroptera; Plecoptera

INTRODUCTION

Small forested streams receive substantial inputs of allochthonous particulate organic matter (leaves, branches, wood) which provide a source of food for many benthic invertebrates. Where the canopy is closed, instream (autochthonous) production may be negligible (Fisher & Likens 1973) and populations of epilithic algae provide only a limited alternative food for browsing species. In larger streams where the canopy opens up, or where forest is replaced by grassland, greater instream primary production can be expected. Under such conditions, living and decomposing algae as well as terrestrially-derived detritus are potentially important foods of the benthos. Their relative importance in the diets of aquatic insects will depend on a variety of factors including the behaviour, mouthpart morphology, and microdistributions of the insects and the ability of the stream to retain organic materials and sustain populations of benthic algae.

The feeding relationships of benthic invertebrates at different sites within a river system have not been investigated in New Zealand. However,

Received 24 June 1983; accepted 22 August 1983

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work on a small beech forest stream in the South Island (Middle Bush Stream, Cass) showed that the animals were mainly coarse- and fine-particle detritivores or predators (Winterbourn 1983). The terrestrial nature of most of the particulate material ingested and assimilated was confirmed by Rounick et al. (1982) and contrasted with the condition in a nearby tussock grassland stream where algae assumed much greater significance in insect diets.

In the present study, the food of numerically dominant benthic insects at 4 sites within a West Coast, South Island river system was examined by gut content analysis. Most of the species considered were abundant at all or several sites (Cowie 1980) so that an excellent opportunity existed to compare ingestion patterns within and between species along the course of the river.

Although gut content analyses enable the larger ingested materials to be identified and described in terms of particle size, they provide no information on their comparative food value or assimilability. Neither is the origin of fine, often amorphous detritus clear from a visual examination, yet it is frequently the most abundant and potentially important food material in the guts of many stream insects. Stable carbon isotope analysis was used in this study to investigate whether carbon incorporated into aquatic insect tissue was of terrestrial or aquatic origin. This was possible since the $^{13}\text{C}/^{12}\text{C}$ ratios of terrestrial plants and aquatic algae can differ significantly (Rounick et al. 1982), and because the tissue ratios of animals reflect those of the foods they eat (DeNiro & Epstein 1978). Insects for stable carbon analysis were collected from the same 4 sites and 2 additional downstream stations.

STUDY AREA

Devils Creek rises at 600–750 m a.s.l. in the foothills of the Victoria Range on the West Coast of the South Island (42°10'S, 171°80'E). It is about 11 km long and flows northwest to enter the Inangahua River 2 km west of Reefton. Its catchment includes part of Tawhai State Forest and in the upper part supports hardwood-beech forest dominated by *Nothofagus* species. Dominant riparian trees within the forest are *Nothofagus menziesii* (Hook. f.) Oerst. and the deciduous *Fuchsia excorticata* (J. E. et G. Forst) Linn. f. Stands of exotic species (mainly *Pinus radiata* D. Don) occur on lower slopes and below them the land has been cleared for farming.

Rainfall at Reefton averages 1920 mm per annum whereas at the Globe Mine in the headwaters of Devils Creek (Fig. 1) it is slightly higher. Heavy falls may occur at any time of year and result in

flash floods and freshets. Water temperature recorded at sites 1–4 during 1977–78 ranged from 2.5 to 17°C and was usually 1–2°C higher at the 2 downstream sites. River water has hardness 30–60 g m⁻³ Ca CO₃, pH 7.1–8.4, and low concentrations of NO₃-N (<0.03 g m⁻³). Further physico-chemical details were given by Cowie (1980).

The benthic fauna was sampled at 5 sites in Devils Creek and its tributaries and in the Inangahua River just above the confluence with Devils Creek (Fig. 1).

Site 1 was in a primary tributary of Oriental Creek in the upper Devils Creek watershed. Bed materials included angular rocks and stones, fine gravel, sand, and silt. Firmly jammed logs were present in the channel which was subjected to heavy scouring during floods.

Site 2 was near the mouth of Oriental Creek, a steep, turbulent stream with a bed dominated by large boulders and exposed slabs of bedrock. The course of the stream channel was irregular and could change markedly after floods. There was no wood debris at this site, and very little leaf litter was retained.

Sites 3, 4, and 5 were in Devils Creek where the valley had broadened so that much of the stream bed was open and unshaded. Site 3 was near the lower limit of hardwood-beech forest, species of *Pinus*, *Eucalyptus*, and *Pseudotsuga* were growing close to the river at Site 4, and Site 5 was bordered by scrub and rough pasture. At low flow, the stream bed at all 3 sites consisted of short, stony riffles alternating with longer runs. The channel was best defined and physically most stable at Site 3 where very large stones (>30 cm) were present. At Site 4 the course of the stream channel changed several times during the period of the study.

Site 6 was in the large Inangahua River about 200 m below the main road bridge at Reefton. Its flat shingle valley was 40–50 m wide and lined by willows (*Salix* spp.), rough pasture, and scrub. Collections were made near the true right margin of the main channel, where the dominant bed materials were loose, smooth, rounded stones (20–40 cm) forming a shallow riffle.

METHODS

Animals for gut content analysis were taken from collections made at Sites 1–4 in April, July, and October 1976 and in January 1977. *Stenoperla prasina* was also collected at Sites 5 and 6 in November 1982 and April 1983. Samples were obtained by the foot-kick method using 2 nets (0.2 mm and 1.0 mm mesh) held in tandem. At all sites an effort was made to collect from all stream habitats in

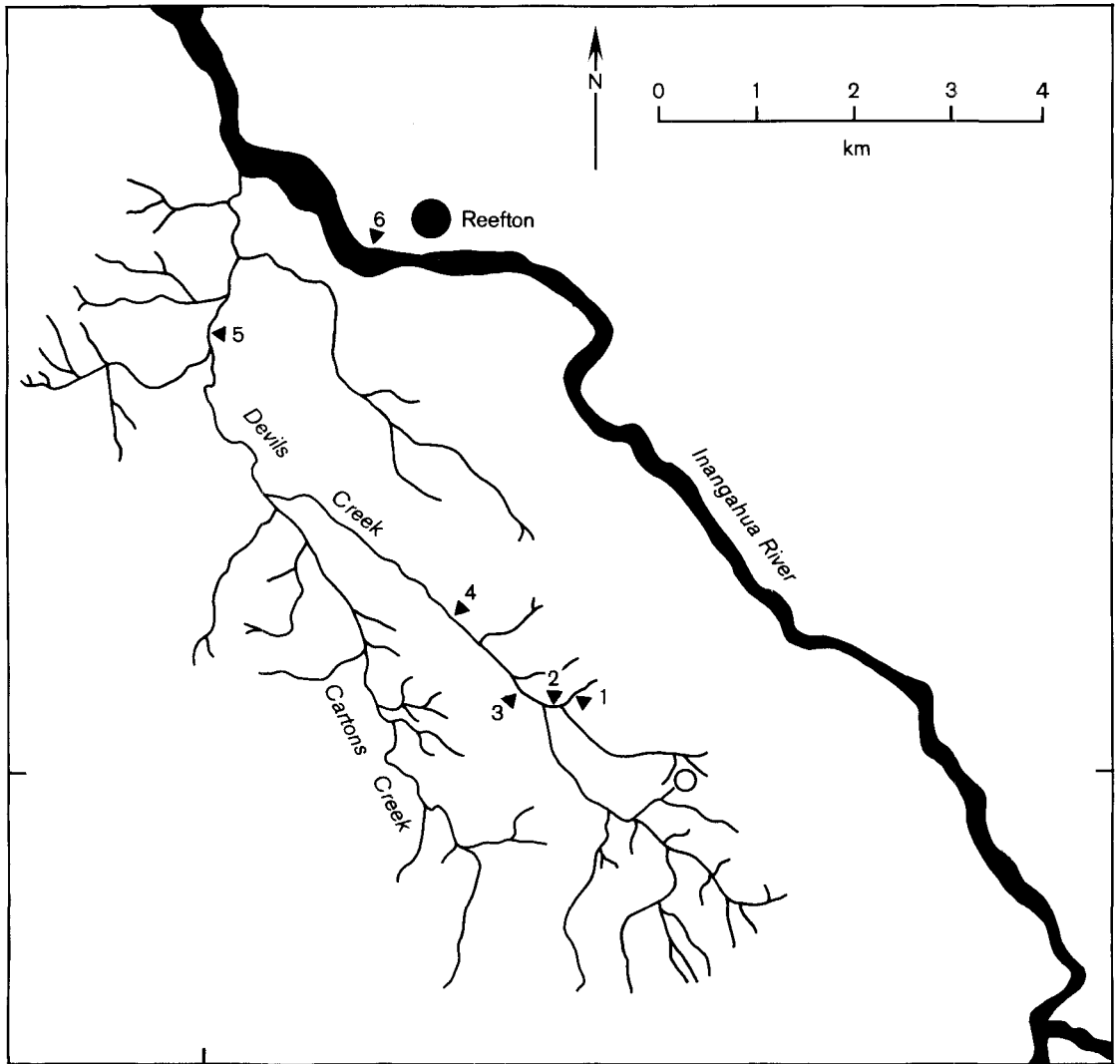


Fig. 1 Map of the Devils Creek system showing numbered sampling sites (▲). Rainfall is measured at the Globe Mine (○).

proportion to their frequency of occurrence. Animals were preserved in 5–10% formalin and later transferred to monoethylene glycol.

Animals for analysis were selected arbitrarily and their headwidths (maximum width across the eyes) were measured at $\times 40$ magnification with a linear eyepiece graticule. Gut contents were removed by microdissection in a drop of water, washed into a plastic vial, and dispersed for 45–60 seconds with an ultrasonic cleaner. They were filtered under vacuum on to an HA Millipore filter ($0.45 \mu\text{m}$) which was mounted on a slide with lactophenol-PVA. Gut

contents of large insect larvae were mounted on separate filters, but for smaller animals contents of up to 6 larvae of similar sizes were pooled. Gut contents of the predatory *S. prasina* were mounted directly on slides without prior dispersion or filtration. Slides were dried for at least a week at 37°C and examined at magnifications up to $\times 450$ with a phase contrast microscope. Contents were assessed on an areal basis with fine particles being assigned to 3 size categories; $0.45\text{--}75 \mu\text{m}$, $75\text{--}250 \mu\text{m}$, and $250 \mu\text{m}\text{--}1 \text{mm}$. Ten randomly selected fields were viewed and the number of eyepiece squares covered

Table 1 Summary of results of gut content analyses made on mayflies, stoneflies and caddisflies from 4 sites in Devils Creek, April 1976–March 1977. F, forested sites 1 and 2; O, open sites 3 and 4. *, < 1%.

	Sites	No. of slides	Mean area of slide covered (%)				
			Fine particles				
			0.45–75 µm	75–250 µm	250µm– 1 mm	Diatoms	Filamentous algae
Ephemeroptera							
<i>Deleatidium</i> spp.	F	30	99	1	–	–	–
	O	36	98	2	–	1	–
<i>Austroclima sepia</i> (Phillips)	F	9	92	8	–	–	–
<i>Nesameletus ornatus</i> (Eaton)	F	8	82	3	–	7	8
	O	12	86	1	–	7	6
<i>Coloburiscus humeralis</i> (Walker)	F	4	97	3	–	–	–
	O	3	94	3	–	–	3
Plecoptera							
<i>Austroperla cyrene</i> (Newman)	F	3	73	27	–	–	–
	O	9	73	24	*	3	*
<i>Spaniocerca zelandica</i> Tillyard	F	14	87	12	–	1	–
	O	7	84	7	–	9	–
<i>Spaniocercoides cowleyi</i> (Winterbourn)	O	2	76	3	–	–	21
<i>Zelandoperla agnetis</i> McLellan	F	6	81	11	–	4	4
	O	8	73	1	–	14	12
<i>Z. fenestrata</i> Tillyard	F	4	60	31	9	–	–
<i>Zelandobius confusus</i> (Hare)	F	6	81	19	–	–	–
	O	7	73	15	–	–	12
Trichoptera							
<i>Pycnocentrella eruensis</i> Mosely	F	2	95	5	–	–	–
<i>Pycnocentria sylvestris</i> McFarlane	F	2	92	8	–	–	–
<i>Olinga feredayi</i> (McLachlan)	O	2	87	10	–	2	1
<i>Aoteapsyche raruraru</i> (McFarlane)	F	3	94	6	–	–	–
<i>Hydrobiosella stenocerca</i> Tillyard	F	2	100	–	–	–	–
	O	3	98	2	–	–	–

by particles in each size category was counted. The proportion of each field covered by algal filaments and diatoms was recorded also. Where possible animal prey were identified to genus and the origin of particles > 75 µm (wood or leaf) determined.

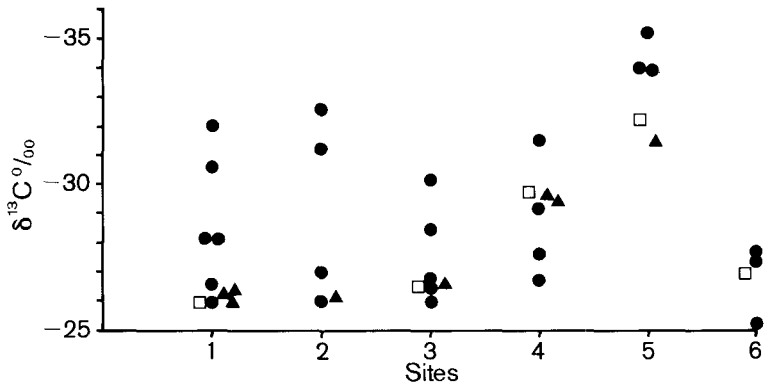
Insects, fine particles, and algae for stable carbon isotope analysis were collected in September and November 1982 and April 1983. Most insects were late instar larvae or pupae (*Pycnocentrella eruensis*) which were frozen soon after collection. Later they were thawed, guts were dissected from larvae to eliminate undigested food, and bodies were freeze-dried. Samples, consisting of up to 10 individuals per species, were prepared and analysed by mass

spectrometry at the Institute of Nuclear Sciences as described by Rounick et al. (1982). Fine particles in 2 size categories (< 500 µm and < 75 µm), stone scrapings, and algae were acidified with 1N HCl before analysis to prevent possible contamination by CaCO₃. ¹³C/¹²C ratios are presented in the conventional δ¹³C notation as ¹³C enrichments relative to the international PDB standard:

$$\delta^{13}\text{C}(\text{‰}) = \left[\frac{^{13}\text{C}/^{12}\text{C} \text{ sample}}{^{13}\text{C}/^{12}\text{C} \text{ standard}} - 1 \right] \times 10^3$$

Analytical precision was ≤ 0.1 ‰ while replicate samples placed randomly in the processing order never differed by more than 0.4 ‰.

Fig. 3 $\delta^{13}\text{C}$ values obtained for benthic insects at 6 sites in Devils Creek and the Inangahua River. ●, collector-browsers; ▲, filter-feeders; □, predators.



most abundant species at their respective sites; gaps in the data set indicate that the species in question were absent or taken in insufficient numbers for analysis.

To provide some indication of intraspecific variability of $\delta^{13}\text{C}$ values which might be expected at a single site, analyses were made of larvae collected from Devils Creek sites in different months, and from forested streams in the nearby Maimai Experimental Catchment Area (Rounick et al. 1982) in different years (Table 4). The average difference in $\delta^{13}\text{C}$ values within species pairs was 1.2 ‰ and the maximum difference was only 2.0 ‰. Such close agreement for a range of species is encouraging for the utility of the method.

$\delta^{13}\text{C}$ values for fine particles in the < 75 μm and < 500 μm classes were in close agreement at all sites and ranged from -26.6 to -27.9 ‰. This indicates that both size classes were dominated by allochthonous material as were stone surface scrapings taken at Sites 5 and 6. In contrast, clean, filamentous algae from Site 5 were depleted in ^{13}C (-34.2 ‰) as was *Cladophora* from Grasmere Stream, Cass (-35.0 ‰; Rounick et al. 1982).

Most benthic invertebrates from the forested sites (1 and 2) and Site 3 had $\delta^{13}\text{C}$ values close to those of fine particles, indicating that they were using carbon sources predominantly of terrestrial origin. Exceptions were *Deleatidium*, *Nesameletus ornatus* (at Site 1), and *Zelandoperla agnetis* (at Site 2) which had more negative $\delta^{13}\text{C}$ values (see discussion). ^{13}C depletion was apparent in most species at Site 4 and at Site 5 it was substantial (Table 3; Fig. 3). From this it can be inferred that autochthonous sources of organic carbon (algae) were being used to a considerable extent at this downstream station. In marked contrast, all species collected from the Inangahua River (Site 6) had $\delta^{13}\text{C}$ values indicating almost total dependence on allochthonous sources of carbon.

DISCUSSION

Despite differences in stream size, gradient, degree of forest cover, and shading, all sites in the Devils Creek system had benthic invertebrate communities dominated by collector-browsers. Insects which can be classified as shredders were absent and filter feeders occurred only in small numbers. In terms of functional feeding groups the faunas at all sites were comparable to those postulated by Cummins (1975) and Vannote et al. (1980) to be typical of open, fifth order, holarctic rivers. Larvae of mayflies and stoneflies were abundant at all sites, with *Deleatidium* spp. numerically dominant at Sites 1, 3, 4, and 5 and *Zelandoperla agnetis* most common at Site 2. Although some species in a total fauna of at least 138 (Cowie 1983) were restricted to forested or open sites, no marked change in community composition was apparent where the stream left the forest (i.e., between Sites 2 and 3).

The absence of shredders, even in the headwater tributary, is not a reflection of a lack of coarse particulate inputs (leaves, bark, branches), but rather of the poor retention of such materials in these physically imposing watercourses whose beds are constantly eroding and shifting as a result of frequent and heavy flooding. Experimental evidence supporting this explanation was given by Rounick & Winterbourn (1983a). Discharge and flow characteristics may also account for the relative paucity of filter feeders in Devils Creek.

Gut contents of all common species examined (except *Stenoperla prasina*) were dominated by fine particles < 75 μm and generally only small differences in the relative abundance of different materials were observed in the guts of larvae taken from Sites 1-4. Detailed gut content analyses of animals from Sites 5 and 6 were not made but larvae of *Deleatidium*, *Coloburiscus humeralis*, and *Nesameletus ornatus* from Site 5, and *Deleatidium*

Table 3 $\delta^{13}\text{C}$ values of algae, stone scrapings, fine particles, and invertebrates from sites in Devils Creek and the Inangahua River (Site 6). C-B, collector-browser; F, filter feeder; P, predator.

	Sites						Feeding mode
	1	2	3	4	5	6	
Fine particles (< 500 μm)	-27.7		-27.8	-27.7	-27.1	-26.6	
Fine particles (< 75 μm)	-27.6	-27.6	-27.3	-26.8	-27.6	-27.9	
Stone scrapings					-28.1	-24.9	
Algae					-34.2		
Ephemeroptera							
<i>Deleatidium</i> spp.	-30.6	-32.6	-30.2	-31.5	-35.2	-27.6	C-B
<i>Nesameletus ornatus</i>	-32.0*		-26.7	-26.8	-34.0	-27.3	C-B
<i>Coloburiscus humeralis</i>	-26.1		-26.6		-31.6		F
Plecoptera							
<i>Stenoperla prasina</i> (Newman)	-26.0*		-26.4*	-29.7*	-32.3	-26.9	P
<i>Austroperla cyrene</i>		-26.0		-29.2			C-B
<i>Spaniocerca zelandica</i>		-27.0	-28.5				C-B
<i>Zelandoperla fenestrata</i>	-25.9						C-B
<i>Z. agnetis</i>	-28.3	-31.2	-26.1	-27.6			C-B
<i>Z. decorata</i> Tillyard						-25.2	C-B
<i>Zelandobius confusus</i>	-26.7		-26.5				C-B
<i>Z. furcillatus</i> Tillyard					-33.9		C-B
Trichoptera							
<i>Pycnocentrella eruensis</i>	-28.3						C-B
<i>Aoteapsyche rarururu</i>	-26.1*	-26.2		-29.6			F
<i>Hydrobiosella stenocerca</i>	-26.2			-29.4			F

* Mean of values given in Table 4.

and *Zelandoperla decorata* from Site 6 in April 1983 contained mainly particles < 75 μm . Similarly, very fine particles were the most abundant material in the guts of insect larvae other than shredders and predators in Middle Bush Stream, Cass (Winterbourn 1983). The slightly greater proportion of larger particles in larger larvae of *Z. agnetis*, *Zelandobius confusus*, *Austroperla cyrene*, and *Spaniocerca zelandica* presumably reflects the greater ability of larger insects to handle and ingest them. In this respect these detritivorous stoneflies resemble many predatory, aquatic larvae in which the upper size limit of prey taken increases with the size of the predator (Peckarsky 1982).

Fine particles collected from all Devils Creek sites were predominantly of terrestrial origin ($\delta^{13}\text{C}$ -27.9 ‰ to -26.6 ‰) as at Middle Bush Stream (Rounick et al. 1982), and stable carbon analyses indicated that with some exceptions so was the carbon incorporated into insect tissue at forested sites. $\delta^{13}\text{C}$ values were lower (more negative) at the more open, downstream sites where stone-surface algal biomass was greater (Cowie 1980) and where diatoms and algal filaments were ingested to some extent. Note also that the trend towards greater ^{13}C depletion at downstream sites was a general one shown not only by collector-browsers but also filter feeders and the predatory *S. prasina*, whose diet was

very similar at all sites. This trend was not continued in the large Inangahua River as would be predicted by the river continuum concept (Vannote et al. 1980), but instead, all species were clearly dependent on terrestrial sources of carbon. The strong flow and mobile bed characteristics of the Inangahua are probably the key to understanding the reasons for this. Because bed materials (predominantly smooth, rounded stones) are continually shifting and being abraded by fine sediments in transport it appears that algal populations have little opportunity to become established and consequently their availability as food for insects is limited. On the other hand, leaves, fragments of wood, and fine particulate material from higher in the catchment and from the extensive, normally dry shingle bed are mobilised during floods and become trapped or settle out downstream as observed at our Site 6. This allochthonous material is being replenished continually and appears to provide the basis for benthic insect production at the Inangahua River site.

The other interesting question whose answer is not immediately apparent is why *Deleatidium*, *N. ornatus*, and *Z. agnetis* from at least some forested sites exhibited ^{13}C depletion relative to other species despite the fact that guts examined contained few algal cells or detritus obviously of algal origin.

Table 4 $\delta^{13}\text{C}$ values of insects collected at the same site on different occasions. DC, Devils Creek; M, Maimai Experimental Catchment Area.

	Site	$\delta^{13}\text{C}$ values	Difference
<i>Nesameletus ornatus</i>	DC1	-31.7; -32.3	0.6
<i>Aoteapsyche raruraru</i>	DC1	-26.0; -26.3	0.3
<i>Stenoperla prasina</i>	DC1	-25.2; -26.8	1.6
	DC3	-26.1; -26.7	0.6
	DC4	-29.2; -30.3	1.1
	M15	-25.3; -27.3	2.0
	M8	-25.9; -27.0	1.1
	M9	-28.7; -30.4	1.7
<i>Deleatidium</i> sp.	M8	-30.4; -32.3	1.9
	M9	-32.9; -34.0	1.1

Larvae of *Deleatidium* and some other insects can feed efficiently on stone-surface organic layers which consist of bacteria, fungi, algae, and small detrital particles embedded in a matrix of slime (Rounick & Winterbourn 1983b). Even though algae may be a minor component of the material ingested by a browsing larva it is likely that algal exudates represent an important source of dissolved organic matter (DOM) taken up by bacteria and other heterotrophs within the stone-surface bio-film (Haack & McFeters 1982). If so, microbes and their slime secretions should possess $^{13}\text{C}/^{12}\text{C}$ ratios corresponding to that of their algal carbon source and so in turn should organic layer feeders even if algae themselves are poorly represented in the diet. A comparable role for dissolved organic carbon released by phytoplankton has been suggested by Cole et al. (1982) who considered it "may be important in regulating microbial growth in oligotrophic aquatic systems."

Bacteria colonising detrital particles which are not incorporated into a distinct stone-surface bio-film are likely to utilise DOM derived from leaf leachates (Dahm 1980; Rounick & Winterbourn 1983b), ground water (Wallis et al. 1981), and other terrestrial sources, at least in the absence of algal blooms (Kaplan & Bott 1982). Therefore, fine particles, dissolved organic carbon, bacteria, and the animals that feed on them should have $\delta^{13}\text{C}$ values in the vicinity of -28‰ . A particularly dramatic demonstration of these 2 carbon pathways is provided by stable carbon data for insects and their potential foods from a very small, slow-flowing stream in the Maimai Experimental Catchment Area (Winterbourn & Rounick unpublished). In this stream, algae were highly depleted in ^{13}C (-39.9‰), indicating use of biogenic (respiration) CO_2 for photosynthesis (Rau 1978; Osmond et al. 1981), and stone-surface dwelling *Deleatidium* larvae which

appeared to ingest few algae were correspondingly depleted in ^{13}C (-41.8‰). In contrast, the $\delta^{13}\text{C}$ value for *Spaniocercoides cowleyi*, a small detritivorous stonefly which was abundant in muddy pools choked with fine particles was -27.5‰ , consistent with that of its detrital food (-28.1‰).

By combining the gut content analysis technique with stable carbon methodology, greater insights into patterns of food use by stream benthos were obtained than if either had been used alone. The importance of allochthonous materials as food was demonstrated at forested and open sites of this physically unstable, flood prone river system, and stable carbon data indicated that algal exudates may be a significant source of carbon incorporated indirectly by organic layer feeders. Although the stable carbon technique essentially provides a summary of an animal's feeding history, the carbon pool of an animal does turn over (Fry & Arnold 1982) so that shifts in autochthonous/allochthonous dependence with time will be reflected by changes in the $^{13}\text{C}/^{12}\text{C}$ ratio. As our analyses were carried out on late larvae and pupae, conclusions reached with respect to food use should not be extended to encompass early life history stages. A profitable objective of future stable carbon studies would be to investigate life history changes in food dependence in streams with differing patterns of primary production and allochthonous inputs.

ACKNOWLEDGMENTS

We thank the New Zealand Forest Service for a grant which supported part of this work, and Dr Colin O'Loughlin, Forest Research Institute, Ilam for permission to work in the Maimai Experimental Catchment Area and stay at the field station.

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