

Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study

James S. Rounick, Michael J. Winterbourn and Graeme L. Lyon

Rounick, J. S., Winterbourn, M. J. and Lyon, G. L. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. – *Oikos* 39: 191–198.

Energy utilization by benthic invertebrates from several New Zealand streams was investigated using stable carbon isotope analysis. $^{13}\text{C}/^{12}\text{C}$ ratios indicated that the faunas of small, forested streams depended primarily on allochthonous sources of carbon whereas variable utilization of allochthonous and autochthonous materials was shown by species from a grassland stream. Relatively ^{13}C -depleted values obtained for the mayfly, *Deleatidium* from forested sites suggest that its larvae assimilate algae selectively. A shift to greater dependence on autochthonous energy sources was shown by invertebrates from small, recently clearcut catchments (1–4 yr) in response to canopy removal and flushing of forest-derived organic materials from the streams. Although coarse in its resolving power, stable carbon isotope methodology provides insights into the trophic linkages within a community and has potential as a management tool.

J. S. Rounick and M. J. Winterbourn, Dept of Zoology, Univ. of Canterbury, Christchurch, New Zealand. G. L. Lyon, Inst. of Nuclear Sciences, Private Bag, Lower Hutt, New Zealand.

Утилизация энергии бентосными беспозвоночными из некоторых рек Новой Зеландии исследовали методом определения стабильных изотопов углерода. Отношение $^{13}\text{C}/^{12}\text{C}$ показало, что животное население мелких лесных рек зависит в первую очередь от аллохтонных источников углерода, и различная степень утилизации аллохтонных и автохтонных материалов показана для видов из рек, луговых сообществ. Относительное снижение содержания ^{13}C установленное у поденок *Deleatidium*, из лесных местообитаний, показывает, что их личинки избирательно ассимилируют водоросли. Увеличение зависимости от автохтонных источников энергии установлено для беспозвоночных из небольших, недавно сформированных водоросльных территорий (1–4 года) в результате сведения лесного покрова и вымывания органического материала лесного происхождения из рек. Методика стабильных изотопов углерода хоть и довольно неточная по своей разрешающей способности, дает представление о трофических связях в сообществе и может использоваться при мониторинге.

Accepted 9 December 1981

© OIKOS 0030-1299/82/050191-08 \$02-50/0

1. Introduction

Trophic relationships of benthic stream invertebrates have been the subject of many studies. Early workers such as Percival and Whitehead (1929), Badcock (1949) and Jones (1950) observed that algae and detritus of both allochthonous and autochthonous origin comprised much of the material ingested by a wide range of species. Several recent studies have stressed the importance of allochthonous inputs as the primary sources of carbon utilized as food in woodland streams (e.g. Minshall 1967, Cummins 1974). However, significant autotrophic production can occur in many streams and rivers (Minshall 1978) and since algal populations turn over rapidly, much dead algal material must enter the detrital pool. In desert streams, detritus of autochthonous origin predominates (Busch and Fisher 1981) whereas in heavily shaded forest streams most detrital material is terrestrial in origin (Fisher and Likens 1973). Most stream environments probably fall between these two extremes and both kinds of detritus undoubtedly occur. The questions arise, can or do particular species utilize both allochthonously and autochthonously derived detritus as food, and if not, are some species restricted to certain kinds of stream for this reason?

The main aim of our study was to investigate the energy utilization of benthic invertebrates in contrasting streams where the relative contributions of allochthonous and autochthonous inputs were markedly different. We approached this problem using stable carbon isotope analysis which has been used successfully for elucidating marine, estuarine and terrestrial food chain relationships (Haines 1976, McConnaughey and McRoy 1979, Tieszen et al. 1979), and for identifying carbon sources in terrestrial (Boutton et al. 1980) and aquatic ecosystems (Rau 1980). In terrestrial ecosystems this is because plants using C_3 and C_4 photosynthesis pathways exhibit distinct carbon isotope ratios (-21 to -33 per mille vs. PDB and -9 to -17 per mille vs. PDB, respectively) (Boutton et al. 1980). Since the $^{13}C/^{12}C$ ratios of terrestrial plants are also distinct from those of aquatic algae (Rau 1980), as a result of the ^{13}C -depleted HCO_3^- source utilized by aquatic plants, this provides a basis for identification of food utilization of aquatic animals. This is because only a small increase in $^{13}C/^{12}C$ has been found in animals relative to their food (DeNiro and Epstein 1978). A further advantage of stable carbon isotope methodology is that animal tissues provide a summary of their previous feeding history, not simply what they ingest (as observed for an instant in time by gut analysis) but what materials are utilized for tissue growth.

A subsidiary aim of this work was to investigate whether large-scale watershed practices (clearcutting and burning) resulting in increased autochthonous primary production were reflected by the $^{13}C/^{12}C$ ratios of the invertebrate fauna.

2. Study sites

Animals and potential foods for stable carbon analysis were obtained from nine streams in the South Island of New Zealand. The principal sites at which the most extensive collections were made were Middle Bush Stream and Grasmere Stream, located about 1 km apart in the Cass basin, western Canterbury ($43^{\circ}02'S$, $171^{\circ}46'E$). Middle Bush Stream drains a 28 ha catchment of subalpine scrub, tussock and bare, scree slope and includes a 3–4 ha stand of mountain beech, *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole through which the stream flows. In the forest, the stream is well shaded (Tab. 1) with a rough boulder



Fig. 1. Upper. A section of Middle Bush Stream in mountain beech forest. Lower. Grasmere stream flowing through tussock grassland.

Tab. 1. Environmental data measured for Middle Bush and Grasmere Streams.

	Middle Bush Stream	Grasmere Stream
Discharge ^a (l s ⁻¹)	4	124
Mean width (m)	1	2.8
Mean depth (m)	0.25	0.40
Alkalinity (µg ml ⁻¹ CaCO ₃)	37.2	34.6
pH	6.8	6.4
Annual temperature range (°C)	1–14	5–17
% Shading	80	5
Light input ^b (langleys d ⁻¹)	14	58
Dominant algal genera . .	<i>Rhoicosphenia</i> , <i>Cocconeis</i>	<i>Cladophora</i> , <i>Melosira</i> , <i>Gomphonema</i>
Algal standing crop ^c g m ⁻²	0.38±SE 0.11	2.94±SE 0.43
Primary course particulate input	Beech	Tussock

a. Mean summer discharge.

b. Estimated for 24 h autumn day using method in Rounick and Gregory (1981).

c. Maximum autumn standing crop levels.

der-strewn bed and steep banks (Fig. 1). Large amounts of coarse particulate allochthonous material, particularly beech leaves and twigs, enter the stream throughout the year (Winterbourn 1976, McCammon 1978) and autochthonous primary production is low (Cowie 1980, unpubl. data). The stream fauna is dominated by larval insects with species of Ephemeroptera, Plecoptera, Trichoptera and Diptera-Chironomidae being most common (see Davis and Winterbourn 1977, Winterbourn 1978).

Grasmere Stream is larger than Middle Bush Stream (Fig. 1, Tab. 1) and for much of its length flows through tussock grassland. Its sources are two small lakes (Sarah and Grasmere) and several beds of *Phormium tenax* J.R. et G. Forst. and *Typha orientalis* G.B. Presl. occur along the upper course. In its middle reaches where collections were made the bed is predominantly gravel and larger stones. The stream supports a high standing crop of benthic algae throughout the year and localized beds of macrophytes including *Elodea canadensis* Michx., *Ranunculus fluitans* Lam., *Potamogeton cheesmanii* A. Benn. and *Myriophyllum propinquum* A. Cunn. The invertebrate fauna is dominated by species of Trichoptera, Ephemeroptera, Chironomidae and a gastropod, *Potamopyrgus antipodarum*.

All additional study sites were located west of the main alpine divide near the towns of Reefton and Ahaura. Callaghans Creek in the Hochstetter State Forest (42°24'S, 171°33'E) is a low-gradient stream similar in size to Middle Bush Stream with a stable, stony bed. Collections were made at two sites, in the

lower reaches where it flows through dense beech forest and is heavily shaded, and in the headwaters where the original vegetation has been replaced 10 yr ago by exotic Monterey pines *Pinus radiata* D. Don.

All other collections were made in small, primary tributaries within the New Zealand Forest Service's Maimai Experimental Catchment Area (see Neary et al. 1978). The streams drain catchments ranging from 1.6 to 8.3 ha, all of which supported beech-podocarp-hardwood forest prior to 1976. Subsequently, a number have been logged and in some cases burnt and replanted with *P. radiata* and eucalypts (*Eucalyptus delegatensis* R.T.B.). Collections were made from two control and four logged catchments (see Tab. 3 for details). All streams had predominantly gravel substrates and very low discharge at the time of sampling (1–4 l s⁻¹), but varied in degree of shading, development of benthic algal populations and inputs of forest litter.

3. Methods

Invertebrates and potential foods for isotope analysis were collected from Middle Bush and Grasmere Streams at intervals over a period of 8 months (October 1980–June 1981). For some insect species, late instar larvae were taken but whenever possible adults and pupae were obtained, as they should provide a summary of an insect's trophic history in their tissues. Both potential foods and animals were preserved soon after collection by freezing; molluscs after they had egested their gut contents. Single collections were made from Callaghans Creek and the Maimai Experimental Catchments in May 1981. They consisted of pupae and late instar larvae as well as potential foods.

Riparian vegetation sampled included pine needles (*P. radiata*), leaves of tussock (*Festuca novae-zelandiae*), beech leaves and beech wood which had been submerged in Middle Bush Stream for 3 yr. Beech leaves were collected from living trees, the forest floor and in water on the stream bed. Samples of three aquatic macrophytes were taken from Grasmere Stream. Fine particulate organic matter (FPOM; 0.45 µm–1.0 mm) was collected at Middle Bush Stream and Grasmere Stream in stone-filled containers which were sunk into the stream beds for a month. At the other sites, FPOM was obtained in sediment cores and passed through a 1 mm mesh sieve. Algae and associated materials were scraped from stones and from glass slides which had been left in the Cass streams for a month. An almost pure algal sample was obtained by thoroughly washing a clump of *Cladophora* from Grasmere Stream.

Leachate for isotope analysis was obtained by soaking preabscission beech leaves in ca. 10 l of non-sterile distilled water for 24 h. The concentrated leachate was filtered (0.45 µm) to remove any FPOM and freeze dried. Finally, one litre samples of Middle Bush and

Grasmere Stream water were collected for dissolved inorganic carbon (DIC) isotope analysis. Water samples were filtered in the field (0.45 μm) and stored in the dark in full, airtight, glass bottles at $<4^{\circ}\text{C}$ for up to 7 d. DIC was precipitated as SrCO_3 from which CO_2 was evolved with acid for mass spectrometric analysis.

In preparation for analysis, materials were unfrozen, and guts dissected from insect larvae to remove undigested food. Any materials suspected of containing carbonates were acidified with 1N HCl. Up to 50 individuals of each species from each site were pooled, freeze-dried, pulverized and stored in a desiccator. At the Institute of Nuclear Sciences laboratory, 3–5 mg subsamples were oxidized in sealed quartz ‘‘vycor’’ tubing using a break-seal method (Buchanan and Corcoran 1959). The resulting CO_2 was purified and analyzed in a Nuclide 6–60 ratio mass spectrometer. Results are reported as the relative per mille difference between the isotope ratio of the sample and that of the international PDB standard (Craig 1957), expressed as follows:

$$\delta^{13}\text{C}_{\text{PDB}} = \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{PDB}}} - 1 \right] \times 1000 \text{ per mille}$$

The more negative the $\delta^{13}\text{C}$ value the greater the ^{13}C depletion. Analytical precision was judged on the basis of eleven replicates of a graphite standard (NBS-21) analyzed over a period of three months ($\bar{X} = -27.99$ per mille, 1 SD = 0.12, range = 0.36). Replicates of potential food and animals placed randomly in the processing order never differed by 0.4 per mille.

4. Results

4.1. Middle Bush Stream

$\delta^{13}\text{C}$ values obtained for invertebrates and allochthonous food materials collected from Middle Bush Stream ranged from -29.5 to -23.9 per mille and -27.3 to -25.0 per mille respectively (Tab. 2). Laboratory produced mountain beech leachate was slightly more ^{13}C -enriched (-25.3 per mille) than the other carbon sources. Beech leaves at different stages of decomposition showed progressive ^{13}C enrichment, ranging from -30.7 per mille for living leaves to -27.3 per mille for those submerged and decomposing in the stream. Beech wood which had been in the stream for 3 yr was even more ^{13}C enriched at -25.0 per mille.

The $^{13}\text{C}/^{12}\text{C}$ ratios of invertebrates from Middle Bush Stream reflected the ratios of allochthonous materials (Tab. 2). *Limonia nigrescens*, a tipulid which inhabits decaying beech logs was most ^{13}C enriched (-23.9 per mille), and its $^{13}\text{C}/^{12}\text{C}$ ratio closely corresponded to that of the wood. Least ^{13}C enrichment was observed in *Deleatidium* sp., a browsing mayfly which was abundant on stones in riffles. The two large, leaf and bark shredding caddisflies, *Oeconesus maori* and *Zelandopsycha ingens* had $\delta^{13}\text{C}$ values close to those of their suspected foods,

as did the leaf-shredding stonefly, *Austroperla cyrene*. All predatory insect larvae possessed ratios close to those of their probable prey.

Stable carbon isotope data from Callaghans Creek (Tab. 2) also indicated a close relationship between allochthonous organic materials and invertebrates in both the beech and pine vegetated sections of the catchment.

4.2. Grasmere Stream

$\delta^{13}\text{C}$ values for potential foods from Grasmere Stream ranged from -35.0 to -23.6 per mille, all materials being depleted in ^{13}C relative to Middle Bush samples with the exception of tussock. Greatest ^{13}C depletion (-35.0 per mille) was found in a sample of filamentous algae from which entrapped fine particles had been washed.

Grasmere Stream invertebrates had $\delta^{13}\text{C}$ values ranging from -35.8 to -29.2 per mille suggesting variable dependence on autochthonous and allochthonous materials as food. *Pycnocentria evecta*, a caddisfly whose browsing larvae ingest large amounts of algae showed the greatest ^{13}C depletion whereas deposit feeding Chironomidae and Oligochaeta were most ^{13}C enriched. $\delta^{13}\text{C}$ values for predatory insects were variable (-32.4 to -29.3 per mille), and an average 5–6 per mille lighter than those for insect predators from Middle Bush Stream. Overall, it is clear that related species from Grasmere Stream showed a higher dependence on autochthonously derived foods (algae, macrophytes) than did those from Middle Bush.

4.3. Maimai experimental catchments

$\delta^{13}\text{C}$ values for common aquatic invertebrate species and their potential foods from tributaries in the Maimai experimental area are shown in Tab. 3. The streams drain catchments which vary in management treatment (burnt or not burnt), age of cut, and time of replanting, factors which could be expected to affect the availability of different foods.

The mayfly *Deleatidium* was most ^{13}C depleted in the earliest logged catchment, and the $\delta^{13}\text{C}$ value of -35.3 per mille indicates that algae were a major source of carbon utilized there. On the other hand, *Deleatidium* from streams in unlogged and more recently logged catchments, where considerable allochthonous debris was still present in the channels, had higher $\delta^{13}\text{C}$ values. These were similar to those found in *Deleatidium* from Middle Bush and Callaghans Creek, and indicated greater allochthonous food dependence. It is of particular interest to note that the same trend was shown also by *Stenoperla prasina*, the major invertebrate predator in these streams. This stonefly probably feeds to a large extent on *Deleatidium* as in other streams (Winterbourn 1974, Devonport and Winterbourn 1976). Shredders were not found in streams draining the earlier-logged catchments where little coarse organic de-

Tab. 2. $\delta^{13}\text{C}$ values of potential foods and invertebrates from four sites. Invertebrate feeding mode is represented as follows: CB- collector-browser; O- omnivore; P- predator; S- shredder.

	Feeding Mode	Middle Bush Stream	Grasmere Stream	Callaghans Creek (Beech forest)	Callaghans Creek (Pine plantation)
Potential Foods					
Beech leaves (living tree)		-30.7			
Beech leaves forest floor		-28.5			
Beech leaves stream conditioned		-27.3			
Beech wood conditioned for 3 yr		-25.0			
Beech leachate		-25.3			
<i>Pinus radiata</i> needles					-29.1
FPOM (< 1 mm > 0.45 μm)		-27.2	-29.1	-28.8	-28.4
Dissolved inorganic carbon		-11.1	-12.1		
Stone organic layer		-26.0	-33.2		
<i>Fissidens rigidulus</i> (C. Müller)		-29.8			
<i>Cladophora</i> sp.			-35.0		
<i>Myriophyllum propinquum</i> A. Cunn.			-26.8		
<i>Elodea canadensis</i> Michx.			-31.1		
<i>Festuca novae-zelandiae</i> Cock.			-23.6		
Invertebrates					
Oligochaeta					
<i>Eiseniella tetraedra</i> (Savigny)	CB	-24.7	-29.3		
Gastropoda					
<i>Potamopyrgus antipodarum</i> (Gray)	CB		-34.5		
Decapoda					
<i>Paraneohrops planifrons</i> White	O			-26.2	
Ephemeroptera					
<i>Coloburiscus humeralis</i> (Walker)	CB		-33.6	-26.1	-27.4
<i>Deleatidium</i> sp.	CB	-29.5	-35.2	-29.2	-29.0
Plecoptera					
<i>Austroperla cyrene</i> (Newman)	S	-26.2			
<i>Spaniocerca zelandica</i> Tillyard	CB	-24.9			
<i>Stenoperla prasina</i> (Newman)	P	-25.9			
<i>Zelandobius confusus</i> (Hare)	CB		-31.1		
<i>Z. furcillatus</i> Tillyard	CB	-23.9			
Megaloptera					
<i>Archichauliodes diversus</i> (Walker)	P			-26.8	-28.4
Trichoptera					
<i>Aoteapsyche colonica</i> (McLachlan)	CB		-33.2		
<i>Edpercivalia maxima</i> (McFarlane)	P	-25.2			
<i>Hudsonema amabilis</i> (McLachlan)	O		-30.7		
<i>Hydrobiosis clavigera</i> McFarlane	P		-32.4		
<i>Hydrobiosella stenocerca</i> Tillyard	CB	-25.5			
<i>Hydrobiosis</i> sp.	P	-25.7	-31.1		
<i>Neurochorema confusum</i> (McLachlan)	P		-29.4		
<i>Oeconesus maori</i> McLachlan	S	-26.1			-28.1
<i>Olinga feredayi</i> (McLachlan)	CB	-25.6	-31.5		
<i>Philorheithrus agilis</i> (Hudson)	P	-24.7			
<i>Polyplectropus puerilis</i> (McLachlan)	O		-30.0		
<i>Psilochorema</i> sp.	P		-29.3		
<i>Pycnocentria evecta</i> McLachlan	CB		-35.8		
<i>Triplectides obsoleta</i> (McLachlan)	S			-28.5	-29.6
<i>Zelandopsyche ingens</i> Tillyard	S	-27.1		-25.6	
Diptera					
Chironomidae					
<i>Limonia nigrescens</i> (Hutton)	S	-23.9	-29.2		
Coleoptera					
Helodidae Species A	CB	-25.9			

Tab. 3. $\delta^{13}\text{C}$ values of potential foods and invertebrates from six catchments in the Maimai Experimental Catchment Area. Feeding modes as in Tab. 2.

Chatchment number Treatment(s)		205 Logged 1978 Planted 1978	206 Control	207 Logged 1976 Burnt 1977 Planted 1977	208 Logged 1979 Burnt 1980 Planted 1980	214 Logged 1977 Burnt 1978 Planted 1978	215 Control
	Feeding Mode						
Potential Foods							
Algae						-32.5	
FPOM		-27.9	-27.2	-28.1	-27.4		-28.1
Invertebrates							
Plecoptera							
<i>Austroperla cyrene</i>	S	-31.8			-25.4		
<i>Stenoperla prasina</i>	P	-29.4		-28.5	-27.0		-27.3
Trichoptera							
<i>Hydrobiosella stenocerca</i>	CB				-25.8		
<i>Oeconesus maori</i>	S				-24.9		
<i>Hydrobiosis</i> sp.	P					-28.5	
<i>Triplectides obsoleta</i>	S	-29.4					
<i>Zelandopsycha</i> sp.	S						-27.8
Ephemeroptera							
<i>Deleatidium</i> sp.	CB	-32.9	-29.3		-30.4	-35.3	-28.5
Megaloptera							
<i>Archichauliodes diversus</i>	P			-27.1			
Decapoda							
<i>Paranehrops planifrons</i>	O	-23.9	-28.6				-25.8

bris remained. $\delta^{13}\text{C}$ values of insects taken from the control and 1979-logged catchments indicated a continued dependence on allochthonous materials whereas some utilization of more ^{13}C -depleted carbon sources by *Triplectides obsoleta* and *Austroperla cyrene* was apparent in the 1978-logged catchment 205.

5. Discussion

The success of this study depended on the existence of a measurable isotopic distinction between allochthonous and autochthonous carbon sources at the study sites. $\delta^{13}\text{C}$ values of potential, allochthonous foods were all about -27 per mille as expected for terrestrial C_3 plants (Boutton et al. 1980).

In contrast, $\delta^{13}\text{C}$ values for algae and aquatic macrophytes approached -35 per mille, a result of the ^{13}C -depleted HCO_3^- source utilized by aquatic plants. Biogenic (respiration) CO_2 , depleted in ^{13}C can also contribute to the inorganic carbon pool utilized by aquatic producers and so lower $\delta^{13}\text{C}$ values further (Rau 1978). However, since $\delta^{13}\text{C}$ values for dissolved inorganic carbon in water samples from Middle Bush and Grasmere Streams (-11.0 and -12.1 per mille, respectively) were within the range expected for river water with isotope exchange with atmospheric carbon dioxide (Mook 1970), it is apparent that biogenic CO_2 was not a significant source of ^{13}C depletion in this study.

The $\delta^{13}\text{C}$ data obtained demonstrated quite clearly the linkages between primary carbon sources and consumers at the study sites. Since they give a summary of

an animal's trophic history, they also offer insights not provided by more traditionally employed methods. While radiotracers can provide information on utilization of selected materials under controlled conditions, they have only limited application in the field. Gut content analyses provide an instantaneous picture of food recently ingested, but tell nothing about the utilization of that food. Stable carbon isotope analysis can overcome some of those limitations, although at least in the way we have been using it, the technique is restricted to evaluation of food relationships at a relatively coarse (i.e. autochthonous vs allochthonous) level. This is because $\delta^{13}\text{C}$ values of potential foods compared must be distinct.

The $\delta^{13}\text{C}$ values for Middle Bush invertebrates, indicated a clear dependence on terrestrial vegetation as food. This was not unexpected as allochthonous materials are generally regarded as being the principal sources of carbon supporting the benthic communities of small, forested streams (e.g. Cummins 1974). However, the relatively ^{13}C -depleted values obtained for *Deleatidium* at all forested sites suggests that this species is less dependent on terrestrial carbon than the other species examined. *Deleatidium* larvae feed on stone surface organic layers which consist of bacteria, fungi, fine particulate detritus, polysaccharide slimes and diatoms. The heterotrophic and allochthonously derived components of the layer would have a $\delta^{13}\text{C}$ value of about -26 per mille whereas the value for diatoms is expected to be about -33 per mille. The larvae appear to ingest materials non-selectively as indicated by gut content analysis (Cowie 1980; authors' unpubl. data). However,

the ^{13}C -depleted values obtained for *Deleatidium* tissue (-29 to -35 per mille) indicate that diatoms are assimilated selectively or more efficiently, a condition which is not apparent from an examination of gut contents alone. This is in accordance with Greig's finding (1976) that *Deleatidium* larvae assimilate diatoms with a high efficiency, ca. 65%. This illustrates one of the strengths of the stable carbon isotope methodology, and is analogous to the findings of Rau and Anderson (1981) that leachate represented an important source of "invisible" carbon incorporated into a laboratory population of the caddisfly *Clistoronia magnifica* (Banks). On the other hand, it should be remembered that the only carbon available for analysis is that which is incorporated into the insect's body tissue. Although, animals do not fractionate the carbon isotope composition of their food (DeNiro and Epstein 1978) it is possible that different foods are utilized in different ways (e.g. incorporation into body tissue or immediate oxidation). Stable carbon ratios will only reflect those sources of food incorporated into body tissue.

In Middle Bush Stream, *Deleatidium* larvae can constitute over 50% of the animals taken in benthic samples and up to 10% of the invertebrate biomass (authors' unpubl. data). This indicates that despite its low standing biomass ($<0.3 \text{ g m}^{-2}$, Tab. 1) algal production can support substantial secondary production. This is possible since turnover of algal populations is rapid in comparison with rates of insect growth (McIntire 1973), and provides further evidence to support Minshall's (1978) view that the role of autotrophs as a source of energy to consumers should not be underestimated in apparently "heterotrophic" streams.

The sources of organic carbon utilized by primarily detritus-feeding invertebrates in Grasmere Stream are more difficult to determine since detritus includes material of algal, aquatic macrophyte and terrestrial origin present in various proportions. The $\delta^{13}\text{C}$ value of -29.1 per mille for the sample of FPOM analysed indicated that it included material of allochthonous and autochthonous origin. Using Rau's (1980) proportional method it can be calculated that the former made up 53–76% depending on the ratio of algal to macrophyte-derived material present. In addition, the composition of FPOM is likely to vary spatially and seasonally, reflecting climatic and phenological phenomena.

Grasmere Stream invertebrates were all depleted in ^{13}C compared with those from forested sites, and the range of $\delta^{13}\text{C}$ values recorded indicate variable dependence on allochthonous and autochthonous materials. This was supported by gut analyses. The gastropod, *Potamopyrgus antipodarum* showed a high level of dependence on algae as a source of carbon ($\delta^{13}\text{C} = -34.5$), and Wisely (1961) suggested that its faeces may represent a major source of food for the filter-feeding mayfly, *Coloburiscus humeralis* in this stream. The plausibility of this suggestion is supported by the stable carbon data (Tab. 2).

Results obtained from the Maimai experimental catchments show the value of stable carbon isotope analysis for investigating trophic responses of stream invertebrate communities to environmental change. Our results, which are of only a preliminary nature, provide an indication of the time scale involved in adjustment by the fauna to a change in energy base. Thus age of cut was important in determining the type of material utilized. The most ^{13}C -depleted insects occurred in the earliest logged catchment (5 yr prior to sampling), reflecting the increased role of algae in their diets. This in turn is a consequence of greater benthic primary production, reduction in forest inputs and the efficient flushing of forest-derived organic materials from the stream by sequential floods. In contrast, stable carbon ratios of invertebrates from the most recently logged catchment (2 yr before sampling) were similar to those of animals from control catchments and indicated little shift in food dependence in this short time.

It is also of interest to note that changes in the nature of the food base following catchment vegetation removal apparently had little impact on the species composition of the Maimai stream communities. Thus, with the exception of the oconesid caddisflies which are obligate large particle detritivores, whose source of food was removed by logging (and in the case of stored materials, floods), no losses or gains of species or marked changes in relative abundance were apparent (unpubl. surveys). This is in contrast to several recent North American studies (e.g. Webster and Patten 1979, Newbold et al. 1980) and in part may be a consequence of the relatively short time which had elapsed since logging. Nevertheless, it is consistent with our observations on the nature of New Zealand stream faunas in general (Winterbourn et al. 1981) which indicate that a nucleus of common genera and species prevail in many streams whether they be in indigenous beech, kauri, or podocarp-hardwood forests, pine plantations or predominantly grassland. Many of these species clearly possess considerable ecological flexibility with respect to habitat requirements, life history patterns, and as indicated by gut analyses and the present work, food requirements. Although plant material of various origins is ingested by many species and converted to animal tissue, it will vary in quality and hence is likely to affect growth as demonstrated by Ward and Cummins (1979) and Fuller and Mackay (1981). If so, differences in growth rates and life history patterns of a species might be expected at different sites reflecting in part the nature and quality of the available carbon sources. Such an explanation could help explain the different life history patterns of stoneflies recorded by Cowie (1980) at forested and open sites within a single New Zealand river system.

In future, refinements and improvements in the application of stable carbon isotope methodology to ecosystem studies are likely to be forthcoming. Analysis of insect larvae at different stages of development, and

at different times of year should enable changes in food dependence within the life history of a species to be assessed. Further it is conceivable that analysis of predators alone could provide a useful "short-cut" method for determining the sources of carbon supporting benthic communities since the $\delta^{13}\text{C}$ values of predators reflect the trophic linkages beneath them. In combination with quantitative field estimates of animal numbers and biomass, $\delta^{13}\text{C}$ data also provides a means by which the energy basis for secondary production can be determined. Because the carbon isotope method discriminates between carbon sources at a relatively coarse level (e.g. allochthonous vs autochthonous), it has limited application in studies of specific food chain linkages. However, because the insights into trophic dependence it provides are broad, and applicable at a community or ecosystem level of investigation, stable carbon analysis would appear to have great potential as a management tool.

Acknowledgements – We thank the New Zealand Forest Service for financial support of this work and for permission to work in the Maimai Experimental Catchment area.

References

- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. – *J. Anim. Ecol.* 18: 193–208.
- Boutton, T. W., Smith, B. N. and Harrison, A. T. 1980. Carbon isotope ratios and crop analyses of *Arphia* (Orthoptera: Acrididae) species in Southeastern Wyoming grassland. – *Oecologia* (Berl.) 45: 299–306.
- Buchanan, D. L. and Corcoran, B. J. 1959. Sealed tube combustion for the determination of carbon-¹⁴ and total carbon. – *Anal. Chem.* 31: 1635–1638.
- Busch, D. E. and Fisher, S. G. 1981. Metabolism of a desert stream. – *Freshwater Biol.* 11: 301–307.
- Cowie, B. 1980. Community dynamics of the benthic fauna in a West Coast stream ecosystem. – Ph.D. Thesis, Univ. of Canterbury, Christchurch, New Zealand.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. – *Geochim. Cosmochim. Acta* 12: 133–149.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. – *BioScience* 24: 631–641.
- Davis, S. F. and Winterbourn, M. J. 1977. Breakdown and colonization of *Nothofagus* leaves in a New Zealand stream. – *Oikos* 28: 250–255.
- DeNiro, M. J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. – *Geochim. Cosmochim. Acta* 42: 495–506.
- Devonport, B. F. and Winterbourn, M. J. 1976. The feeding relationships of two invertebrate predators in a New Zealand river. – *Freshwater Biol.* 6: 167–176.
- Fisher, S. G. and Likens, G. E. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. – *Ecol. Monogr.* 43: 43–58.
- Fuller, R. L. and Mackay, R. J. 1981. Effects of food quality on the growth of three *Hydropsyche* species (Trichoptera: Hydropsychidae). – *Can. J. Zool.* 59: 1133–1140.
- Greig, C. A. 1976. Ecology of *Deleatidium* sp. (Ephemeroptera) in Lake Grasmere, Canterbury, with particular reference to its trophic relationships. – M.Sc. Thesis, Univ. of Canterbury, Christchurch, New Zealand.
- Haines, E. B. 1976. Stable carbon isotope ratios in the biota, soils and tidal waters of a Georgia salt marsh. – *Est. Coast. Mar. Sci.* 4: 609–616.
- Jones, J. R. E. 1950. An ecological study of the River Towy. – *J. Anim. Ecol.* 19: 68–86.
- McCammon, R. G. 1978. Organic energy flow in a mountain beech forest stream ecosystem. – M.Sc. Thesis, Univ. of Canterbury, Christchurch, New Zealand.
- McConnaughey, T. and McRoy, C. P. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. – *Mar. Biol.* 53: 257–262.
- McIntire, C. D. 1973. Periphyton dynamics in laboratory streams, a simulation model and its implications. – *Ecol. Monogr.* 43: 399–420.
- Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland spring brook community. – *Ecology* 48: 139–149.
- 1978. Autotrophy in stream ecosystems. – *BioScience* 28: 767–771.
- Mook, W. G. 1970. Stable carbon and oxygen isotopes of natural waters in The Netherlands. – In: *Proceedings, Isotope Hydrology*. International Atomic Energy Agency, Vienna, pp. 163–190.
- Neary, D. G., Pearce, A. J., O'Loughlin, C. L. and Rowe, L. K. 1978. Management impacts on nutrient fluxes in beech-podocarp-hardwood forests. – *N.Z. J. Ecol.* 1: 19–26.
- Newbold, J. D., Erman, D. C. and Roby, K. B. 1980. Effects of logging on macroinvertebrates in streams with or without buffer strips. – *Can. J. Fish. Aquat. Sci.* 37: 1076–1085.
- Percival, E. and Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. – *J. Ecol.* 17: 282–314.
- Rau, G. H. 1978. Carbon-13 depletion in a subalpine lake: Carbon flow implications. – *Science* 201: 901–902.
- 1980. Carbon-13/Carbon-12 variation in subalpine lake aquatic insects: Food source implications. – *Can. J. Fish. Aquat. Sci.* 37: 742–746.
- and Anderson, N. H. 1981. Use of $^{13}\text{C}/^{12}\text{C}$ to trace dissolved and particulate organic matter utilization by populations of an aquatic invertebrate. – *Oecologia* (Berl.) 48: 19–21.
- Rounick, J. S. and Gregory, S. V. 1981. Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. – *Hydrobiologia* 83: 197–205.
- Tieszen, L. L., Hein, D., Qvortrup, S. A., Troughton, J. H., and Imbamba, S. K. 1979. Use of $\delta^{13}\text{C}$ values to determine vegetation selectivity in East African herbivores. – *Oecologia* (Berl.) 37: 351–359.
- Ward, G. M. and Cummins, K. W. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). – *Ecology* 60: 57–64.
- Webster, J. R. and Patten, B. C. 1979. Effects of watershed perturbations on stream potassium and calcium dynamics. – *Ecol. Monogr.* 49: 51–72.
- Winterbourn, M. J. 1974. The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. – *Freshwater Biol.* 4: 507–524.
- 1976. Fluxes of litter falling into a small beech forest stream. – *N.Z. J. Mar. Freshwater Res.* 10: 399–416.
- 1978. The macroinvertebrate fauna of a New Zealand forest stream. – *N.Z. J. Zool.* 5: 157–169.
- , Rounick, J. S. and Cowie, B. 1981. Are New Zealand stream ecosystems really different? – *N.Z. J. Mar. Freshwater Res.* 15: 321–328.
- Wisely, B. 1961. Studies on Ephemeroptera I. – *Coloburiscus humeralis* (Walker); Early life history and nymph. – *Trans. Roy. Soc. N.Z.* 1: 249–257.