

## Food webs in forest and pasture streams in the Waikato region, New Zealand: a study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents

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**Abstract** Stable isotopes of carbon (C) and nitrogen (N) were studied in 11 stream communities in the Waikato region of New Zealand. From comparisons of mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, food webs in the shaded, forest streams were clearly based on allochthonous material (conditioned leaf litter and terrestrial invertebrates). Autotrophs in forest streams were not a significant C source for the food webs. However, the C source of food webs in the unshaded pasture streams appeared to be a mixture of allochthonous and autochthonous material. Conditioned leaf litter appeared to contribute to the pasture stream food webs, and the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of some samples of epilithic diatoms indicated their consumption by invertebrates in pasture streams. Fish ate a wide range of aquatic invertebrates; longfinned eels (*Anguilla dieffenbachii*) and banded kokopu (*Galaxias fasciatus*) also had a large proportion of terrestrial invertebrates in their diet. Filamentous green algae were found only at pasture sites, where they were sometimes abundant. The wide range of  $\delta^{13}\text{C}$  values of filamentous green algae (–18.8 to –29.7‰) complicated understanding of their role in the stream food webs. The  $\delta^{13}\text{C}$  values of *Cladophora* were related to water velocity, with more  $^{13}\text{C}$ -enriched values in pools than in runs (–23.2‰ in pools, mean velocity 0.12 m s<sup>-1</sup>; –28.1‰ in runs, mean velocity 0.24 m s<sup>-1</sup>). Crayfish and the gastropod mollusc *Potamopyrgus* appeared to be the only invertebrates to eat filamentous green algae.

**Keywords** stable isotopes; carbon; nitrogen; invertebrates; fish; food webs; land use

### INTRODUCTION

In the Waikato region of New Zealand, biomass of fish and eel production has been related to land use. Pasture streams had much greater fish biomass and eel production than forested streams (Hicks & McCaughan 1997), and pasture streams also had the greater primary production (Quinn et al. 1997a). The aim of this project was to investigate the influence of land use on food webs in streams in the Waikato region. Food webs in streams begin with inputs of organic and inorganic carbon (C) and light, and food web components may include algae, leaf litter, non-predatory and predatory invertebrates, and fish (e.g., Rounick & Winterbourn 1986). Catchment vegetation, especially in the riparian zone, has a major influence on food webs in streams, through both shading and litter inputs (e.g., Vannote et al. 1980; Cummins et al. 1989; Gregory et al. 1991).

Food webs were studied by tracing the fractionation of stable isotopes of C ( $^{12}\text{C}$  and  $^{13}\text{C}$ ), and nitrogen (N) ( $^{14}\text{N}$  and  $^{15}\text{N}$ ), and by examining the gut contents of fish. The basis of the isotope technique is that enzymatic and diffusion processes discriminate against the heavier isotopes of both C and N, resulting in a predictable change in isotopic ratio in the consumer compared to the source (Griffiths 1991). The use of both C and N isotopes together improves the resolution of food webs compared to analysis of C isotopes alone (Peterson & Fry 1987; Fry 1991), and overcomes some of the criticisms recently aimed at isotope food-web analyses by France (1995a; 1996a,b,c).

### Isotopic ratios of carbon

The importance of allochthonous C compared to autochthonous C as a base for secondary production can theoretically be determined from the  $\delta^{13}\text{C}$  of

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the consumers. Allochthonous C derived from terrestrial plants with the C<sub>3</sub> photosynthetic pathway generally has a  $\delta^{13}\text{C}$  value of -26 to -29‰, c. 20‰ less than the  $\delta^{13}\text{C}$  value of atmospheric CO<sub>2</sub> (-8‰; O'Leary 1988). Diffusion and photosynthesis discriminate against <sup>13</sup>C, the heavier stable isotope of C. In water, HCO<sub>3</sub><sup>-</sup> can act as a C source. Since the  $\delta^{13}\text{C}$  of HCO<sub>3</sub><sup>-</sup> can be 9‰ more negative than dissolved CO<sub>2</sub>, photosynthesis using HCO<sub>3</sub><sup>-</sup> can result in aquatic plant tissue that has  $\delta^{13}\text{C}$  values of c. -35‰ (e.g., Rau 1980; Rounick & Hicks 1985).

In practice, the  $\delta^{13}\text{C}$  values of terrestrial and aquatic is quite variable. Substrate limitation can overcome enzymatic discrimination, resulting in less negative  $\delta^{13}\text{C}$  values than expected. Carbon in the leaves of terrestrial plants may vary seasonally in  $\delta^{13}\text{C}$  by 5‰ in response to stomatal closure at times of water stress (Walcroft et al. 1997). High irradiance can cause terrestrial leaves to be less negative in  $\delta^{13}\text{C}$  than leaves photosynthesising at low irradiance; leaves in the upper canopy can be 3-4‰ less negative than leaves in the lower canopy (Ehleringer et al. 1986; Schlessler 1990, 1992).

Aquatic plants photosynthesising in water also show seasonal variability in  $\delta^{13}\text{C}$  (Boon & Bunn 1994). In lake phytoplankton, high rates of photosynthesis lead to substrate limitation and  $\delta^{13}\text{C}$  values close to 0‰ (McCabe 1985). Despite this variability, aquatic plants often have different values of  $\delta^{13}\text{C}$  than land plants (O'Leary 1988), which enables determination of whether a food web is principally based on land plants or in-stream primary production (e.g., Rounick et al. 1982; Winterbourn et al. 1984; Rounick & Hicks 1985). Where isotopic signatures of C sources do not follow predictions, the results may still usefully indicate testable hypotheses concerning ecosystem function.

The C ratio of each consumer should reflect its assimilated C, with an enrichment in <sup>13</sup>C caused by the assimilatory and respiratory processes that use <sup>12</sup>C preferentially. The  $\delta^{13}\text{C}$  of the consumer can be 0-1‰ less negative than its food (Peterson & Fry 1987). White muscle of rainbow trout (*Oncorhynchus mykiss*) aged 0-2 years and fed on trout pellets was 0.9-1.7‰ less negative than their food; enrichment declined with age and size (Rounick & Hicks 1985). A similar decline of <sup>13</sup>C enrichment with increasing size was observed in brook char (*Salvelinus fontinalis*, Peterson & Howarth 1987).

### Isotopic ratios of nitrogen

The ratio of <sup>15</sup>N/<sup>14</sup>N in air is relatively invariant (Mariotti 1983), and is the defined zero point. Leaves of terrestrial plants may range in  $\delta^{15}\text{N}$  from -8 to +3‰, and where aquatic plants have different values to those of terrestrial plants that might contribute litter to a stream, N isotopes may function as source markers for tracing the autochthonous or allochthonous origin of N in food webs, augmenting information from the ratio of <sup>13</sup>C/<sup>12</sup>C (Peterson & Fry 1987; France 1995b). Nitrogen fixation also affects the  $\delta^{15}\text{N}$  of N sources, resulting in organic N that is  $\delta^{15}\text{N}$  0.6-4.1‰ more negative than the N source. Values in plant tissues reflect their N source (Handley & Raven 1992; France 1995b).

Nitrogen in most parts of the biosphere has  $\delta^{15}\text{N}$  values ranging from -10 to +10‰, primarily because the N uptake by plants and microbes is limited by supply rather than by enzymatic uptake (Peterson & Fry 1987). However, subsequent fractionation is greater for <sup>15</sup>N than for <sup>13</sup>C, frequently resulting in a c. 3‰ increase in  $\delta^{15}\text{N}$  between trophic levels (Peterson & Fry 1987; Handley & Raven 1992).

### STUDY AREAS

Study sites in the Waikato region were located on streams draining native forest (three sites), exotic forests of *Pinus radiata* (four sites), and pasture lands (four sites). The physical characteristics of the sites have been previously reported (Hicks & McCaughan 1997). The fish populations of these streams were dominated by longfinned eels (*Anguilla dieffenbachii*), though shortfinned eels (*A. australis*) were also abundant at pasture sites (Hicks & McCaughan 1997). Banded kokopu (*Galaxias fasciatus*) occurred at forested sites, and Cran's and redfinned bullies (*Gobiomorphus basalis* and *G. huttoni*) were found at exotic forest and pasture sites. Common smelt (*Retropinna retropinna*) occurred at one pasture site only. The freshwater crayfish (*Paranephrops planifrons*) was common at all sites.

### MATERIALS AND METHODS

The majority of samples were collected in January and early February 1993, and from one site in January 1994. Some additional invertebrates samples used to make up a core group at each site

were collected late March and early April 1993. Supplementary watercress (*Rorippa nasturtium-aquaticum*), algal, and molluscan samples were collected from site PW2 in early March 1995 by S. E. Bunn (Griffith University, Queensland, Australia). On collection, samples were stored at 0°C in crushed ice for transport to the laboratory within 3 h. Fish guts were removed and preserved in 10% formalin before analysis. White muscle was cut from the fish and oven-dried to a constant weight at 40°C, which usually required 24 h. Muscle from the tails of crayfish was removed from the exoskeleton and oven-dried for 24 h at 40°C. Other invertebrates and conditioned leaf litter were similarly dried whole. Guts were not removed from the invertebrates. After drying, leaf material from woody plants was ground in a ball mill to a fine, homogeneous powder. Algal and animal tissues were ground under liquid N<sub>2</sub> with a mortar and pestle. The molluscan scrapers *Latia* and *Potamopyrgus* were ground whole, with their shells, except for the 1995 sample in which some were first acid-washed.

Among the invertebrates, the largest sized individuals were selected for stable isotope analysis. Total lengths of fish analysed were 95–242 mm (mean 166 mm,  $N = 8$ ) for banded kokopu, 54–92 mm (mean 71 mm,  $N = 17$ ) for Cran's bullies, 178–987 mm (mean 411 mm,  $N = 79$ ) for longfinned eels, and 109–498 mm (mean 288 mm,  $N = 40$ ) for shortfinned eels. Fork length was 79–85 mm (mean 83 mm,  $N = 5$ ) for common smelt. The size range of crayfish sampled for stable isotopes was 5.1–36.3 mm OCL (orbit-carapace length; mean 19.4 mm,  $N = 68$ ). These size data were pooled across all land-use types.

### Isotopic fractionation

Water samples were analysed for dissolved inorganic C (DIC) concentration and  $\delta^{13}\text{C}$  using the methods of McCabe (1985). Measurements of isotopic ratios were made using a VG Micromass 602E mass spectrometer with double ion-collection and inlet systems, equipped for rapid switching between standard and samples for high accuracy and precision. For measuring biotic samples, where lower accuracy and precision was acceptable, a Europa Scientific Tracermass mass spectrometer with a single ion-collector and inlet system was used. Small subsamples (3–6 mg) of dried, ground material were weighed with a 5-place balance, and oxidised at high temperature in the furnace of a Carlo Erba CHNO analyser gas chromatograph. The

resultant CO<sub>2</sub> or N<sub>2</sub> stream was then analysed with the Tracermass to a precision of c. 0.1‰ for <sup>13</sup>C and 0.3‰ for <sup>15</sup>N. Correction for drift was made automatically by the Tracermass from a reference sample of known fractionation measured every 40 or so samples.

The ratios of <sup>13</sup>C/<sup>12</sup>C and <sup>15</sup>N/<sup>14</sup>N were expressed as relative difference per mil (‰) using the equation:

$$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

where  $X = ^{13}\text{C}$  or <sup>15</sup>N, and  $R = ^{13}\text{C}/^{12}\text{C}$  or <sup>15</sup>N/<sup>14</sup>N. The ratio of <sup>13</sup>C to <sup>12</sup>C was compared to the PDB standard, for which  $R_{\text{standard}} = 1.1237$  atom % <sup>13</sup>C (Craig 1957). For <sup>15</sup>N/<sup>14</sup>N, N<sub>2</sub> in air was used as the standard, and  $R_{\text{standard}} = 0.3663$  atom % <sup>15</sup>N (Mariotti 1983).

### Data analysis

To find group means for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , the food-web components were assigned *a priori* to the various consumer groups. Assignment to consumer groups was made on the basis of previous studies (Rounick et al. 1982; Winterbourn 1982; Winterbourn et al. 1984; Linklater 1991; Quinn et al. 1992; Linklater & Winterbourn 1993), except for *Ichthyobotus*, which was classified as a predator on the basis of its large, tusk-like mandibles. Values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were compared among land-use types using Kruskal-Wallis nonparametric one-way analysis of variance, which reduces to a Mann-Whitney  $U$  test for two samples, and Tukey's multiple comparison test (Zar 1984; Wilkinson et al. 1994).

## RESULTS

### Stable isotope ratios

Leaf litter was the most <sup>15</sup>N-depleted food web component in all land-use types (Table 1). Dual isotope plots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  showed that leaf litter was the primary C source of food webs in forest streams (Fig. 1). Epilithic diatoms were an insignificant food source in forest streams, as shown by their <sup>15</sup>N-enrichment and <sup>13</sup>C-depletion compared to other food-web components. However, in pasture streams the distinction between leaf litter and epilithic diatoms as a C source was less clear (Fig. 1). The wide variation in  $\delta^{13}\text{C}$  suggests that although diatoms were probably a food source in some pasture streams, in other pasture streams the

sampled diatoms were too enriched in  $^{13}\text{C}$  to be a significant C source. Filamentous green algae were found only in pasture streams, and also showed a considerable range of  $\delta^{13}\text{C}$  values, but were on average too enriched in  $^{15}\text{N}$  to be a food of the non-predatory invertebrates. However, crayfish in pasture streams appeared likely to have consumed filamentous algae (Fig. 1). The  $\delta^{13}\text{C}$  and  $^{15}\text{N}$  values of the single moss sample from a pasture stream

showed that it was unlikely to have been a significant C source.

Fish were the top aquatic consumers because they had the highest mean  $\delta^{15}\text{N}$  values in all land uses (Fig. 1). The mean  $\delta^{13}\text{C}$  of fish (all species combined) were very similar among land-use types, despite the differences in  $\delta^{13}\text{C}$  of the leaf litter in each land-use type. The range of  $\delta^{13}\text{C}$  in all 129 fish measured was  $-22.9$  to  $-28.4\%$ . Crayfish were

**Table 1** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of putative carbon (C) sources and a priori consumers in streams in native forest (NF), exotic forest (EF), and pasture (PA) in the Waikato region, New Zealand, in summer 1993.

Consumer group	Taxon	Land-use type	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
			N	Mean	N	Mean
<b>Conditioned leaf litter</b>		NF	9	-29.7	18	-1.4
		EF	12	-29.1	24	-0.2
		PA	14	-27.2	28	2.4
<b>Primary producers</b>						
Epilithic diatoms		NF	3	-32.3	3	10.1
		EF	4	-31.6	4	7.4
		PA	4	-24.6	4	3.8
Filamentous green alga	<i>Cladophora</i>	PA	10	-26.3	10	6.4
Filamentous green alga	<i>Spirogyra</i>	PA	3	-20.3	3	1.9
Moss		PA	1	-33.0	1	6.9
Filamentous red alga	<i>Batrachospermum</i>	EF	1	-40.1		
<b>Non-predatory invertebrates: herbivores and detritivores</b>						
Oligochaete		EF	2	-26.1	2	2.9
		PA	4	-26.2	4	4.3
Amphipod	<i>Paracalliope fluviatilis</i>	EF	1	-27.2	1	-0.5
Mayfly	<i>Coloburiscus</i>	NF	9	-26.9	9	3.2
		EF	13	-27.3	13	4.2
		PA	4	-26.2	3	5.0
Mayfly	<i>Deleatidium</i>	NF	3	-29.1	2	1.6
		EF	4	-29.8	3	4.8
		PA	4	-27.6	4	4.4
Mayfly	<i>Nesameletus</i>	NF	5	-32.7	5	3.0
		EF	6	-33.3	5	5.9
		PA	9	-25.7	9	5.0
Mayfly	<i>Siphlaenigma</i>	EF	1	-25.6	1	3.7
Mayfly	<i>Zephlebia</i>	NF	3	-27.0	3	2.0
		EF	7	-26.7	7	4.0
		PA	1	-28.7	1	4.9
Net-spinning caddis	Hydropsychidae	NF	3	-27.1	3	1.8
		EF	4	-27.0	4	5.8
		PA	1	-25.9		
Cased caddis	<i>Pycnocentria evecta</i>	PA	1	-27.7	1	3.9
Non-biting midge	Chironomid	PA	1	-29.0		
Pulmonate mollusc	<i>Latia</i>	NF	1	-23.4	1	1.9
		EF	8	-24.1	8	7.9
		PA	1	-23.4	1	5.8
Gastropod mollusc	<i>Potamopyrgus</i>	NF	3	-15.9	3	4.3
		EF	3	-16.1	3	5.4
		PA	13	-18.4	13	4.5

always more enriched in  $^{13}\text{C}$  than fish, but were less enriched in  $^{15}\text{N}$  (Fig. 1), suggesting that they ate primarily invertebrates, but that they probably also ate a variety of other foods. OCL explained <6% of the variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The increase in  $\delta^{13}\text{C}$  between leaf litter and fish was greater in forest sites than in pasture, and was 4.7‰ in native forest (–29.7 to –25.0‰), 4.0‰ in exotic forest (–29.1 to –25.1‰), and 2.0‰ in pasture (–27.3 to –25.3‰). The average increase in  $\delta^{13}\text{C}$  per trophic step across the three steps between leaf litter, non-predatory invertebrates, predatory invertebrates, and fish was 1.6‰ in native forest, 1.3‰ in exotic forest, and 0.6‰ pasture.

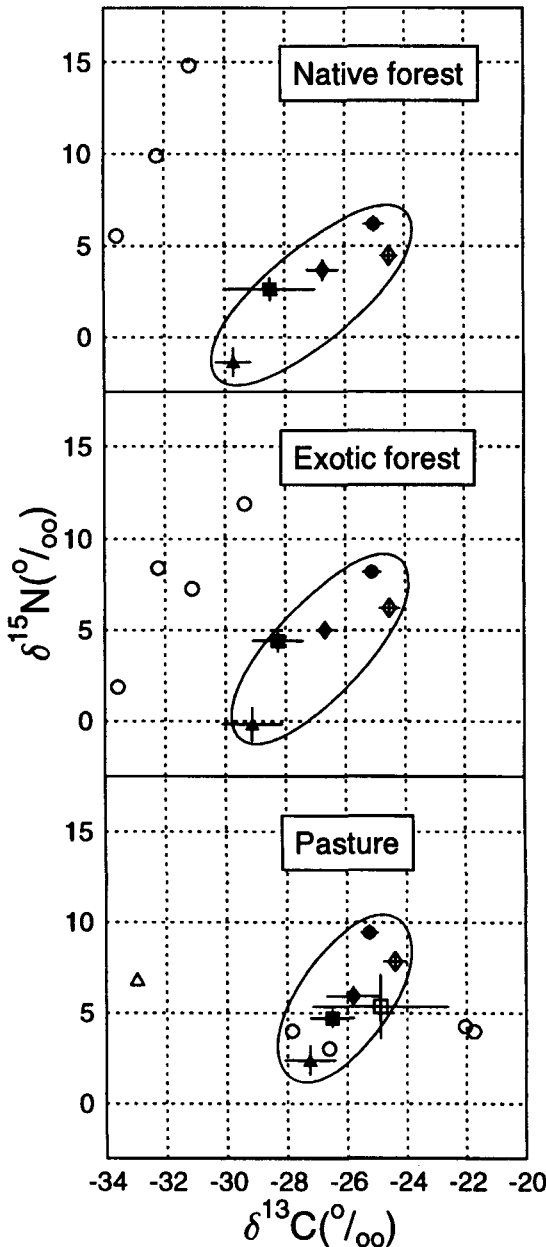
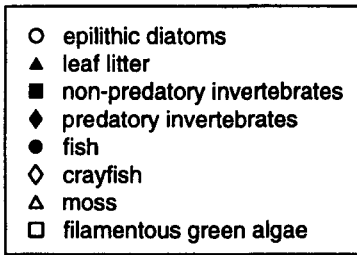
The difference in  $\delta^{15}\text{N}$  between predatory and non-predatory invertebrates other than crayfish

suggests some degree of omnivory, or incorrect *a priori* classification to consumer groups. The increase in  $\delta^{15}\text{N}$  between leaf litter and fish was similar in all land-use types. The increases were 7.5‰ in native forest (–1.3 to 6.2‰), 8.4‰ in exotic forest (–0.2 to 8.2‰), and 7.0‰ in pasture (2.4 to 9.4‰). The average increase in  $\delta^{15}\text{N}$  per trophic step across the three steps between leaf litter, non-predatory invertebrates, predatory invertebrates, and fish was 2.5‰ in native forest, 2.8‰ in exotic forest, and 2.3‰ pasture.

Conditioned leaf litter and epilithic diatoms were more  $^{13}\text{C}$ -enriched at pasture sites than at forested sites (Table 1, 2). This trend was also shown by the collector-browsers *Deleatidium* and *Nesameletus*, and the net-spinning caddises of the

**Table 1** (continued).

Consumer group	Taxon	Land-use type	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
			N	Mean	N	Mean
<b>Predatory invertebrates: first-level carnivores</b>						
Mayfly	<i>Ameletopsis</i>	NF	4	–27.7	4	4.1
		EF	2	–26.7	2	5.3
Burrowing mayfly	<i>Ichthybotus</i>	NF	2	–26.3	2	3.7
		EF	4	–26.6	4	4.8
Dragonfly	<i>Antipodochlora</i>	EF	2	–27.2	2	4.5
		PA	1	–29.1	1	5.1
Dobsonfly	<i>Archichauliodes</i>	NF	6	–26.2	5	3.8
		EF	13	–26.6	13	4.8
		PA	9	–25.1	8	5.7
Free-living caddis	<i>Hydrobiosis</i>	NF	1	–27.4	1	2.4
		PA	8	–26.1	7	5.9
Stonefly	<i>Stenoperla</i>	NF	3	–26.6	3	3.5
Flatworm	Turbellaria	NF	1	–26.6		
		EF	3	–26.8	2	6.7
		PA	2	–26.2	2	7.4
<b>Fish: second-level carnivores</b>						
Longfinned eel	<i>Anguilla diffebachii</i>	NF	21	–25.3	21	6.7
		EF	28	–25.2	28	8.4
		PA	22	–25.6	22	9.4
Shortfinned eel	<i>Anguilla australis</i>	NF	6	–24.4	6	6.1
		EF	7	–23.9	7	8.6
		PA	21	–25.2	21	8.9
Banded kokopu	<i>Galaxias fasciatus</i>	NF	7	–24.6	7	5.0
		EF	1	–26.1	1	6.9
Cran's bully	<i>Gobiomorphus basalis</i>	EF	6	–25.6	6	7.6
		PA	4	–24.7	4	8.6
Redfinned bully	<i>Gobiomorphus huttoni</i>	EF	1	–25.6	1	6.3
Common smelt	<i>Retropinna retropinna</i>	PA	5	–24.3	5	12.3
<b>Omnivores</b>						
Crayfish	<i>Paranephrops planifrons</i>	NF	22	–24.5	22	4.5
		EF	23	–24.5	23	6.2
		PA	22	–24.4	22	7.8



family Hydropsychidae. In forested streams, *Nesameletus* was by far the most <sup>13</sup>C-depleted of any invertebrate. This suggests that primary food of *Nesameletus* might have been the similarly <sup>13</sup>C-depleted epilithic diatoms, but the higher δ<sup>15</sup>N values of the diatoms show that diatoms could not have been the sole food. *Deleatidium*, *Zephlebia*, *Latia*, and flatworms were not significantly different in δ<sup>13</sup>C or δ<sup>15</sup>N among land-use types (Table 1, 2).

**Table 2** Probabilities (*P*) for Kruskal-Wallis of significance of differences in δ<sup>13</sup>C and δ<sup>15</sup>N among land-use types for trophic groups in forest and pasture streams in the Waikato region, New Zealand.

Trophic group	<i>P</i>	
	δ <sup>13</sup> C	δ <sup>15</sup> N
Conditioned leaf litter	0.001	<0.001
Epilithic diatoms	0.025	0.116
<i>Coloburiscus</i>	0.027	0.009
<i>Deleatidium</i>	0.192	0.105
<i>Nesameletus</i>	0.003	0.104
<i>Zephlebia</i>	0.220	0.095
Hydropsychidae	0.032	0.034
<i>Latia</i>	0.285	0.169
<i>Potamopyrgus</i>	0.023	1.000
<i>Archichauliodes</i>	0.002	0.003
Flatworms	0.439	0.121
Longfinned eels	0.539	<0.001
Shortfinned eels	0.007	0.001
Crayfish	0.551	<0.001

**Table 3** Dissolved inorganic carbon (DIC) in streams in exotic forest, native forest, and pasture in the Waikato region, New Zealand. (CL = 95% confidence limit.)

Land-use type	<i>N</i>	DIC (millimol litre <sup>-1</sup> )		
		Mean	Lower CL	Upper CL
<b>DIC concentration</b>				
Native forest	5	0.21	0.15	0.27
Exotic forest	6	0.16	0.13	0.19
Pasture	8	0.22	0.21	0.24
δ <sup>13</sup> C				
<b>Stable carbon isotopic composition of the DIC</b>				
Native forest	6	-14.2	-15.3	-13.0
Exotic forest	6	-13.0	-15.5	-10.5
Pasture	7	-16.5	-19.0	-13.9

◀ **Fig. 1** Mean fractionation of stable carbon (C) and nitrogen (N) isotopes by presumed consumer categories in streams grouped by land-use type in forest and pasture in the Waikato region of New Zealand. Vertical and horizontal bars are 95% confidence intervals. Ellipse for each land use defines the main path of isotopic fractionation.

However, *Potamopyrgus* was more negative in  $\delta^{13}\text{C}$  at pasture sites than at forested sites, reflecting the lower  $\delta^{13}\text{C}$  of DIC at pasture sites that was incorporated into the non-dietary C in its shell (Table 3B). The  $^{13}\text{C}$ -enrichment of *Latia* also showed contamination with non-dietary C.

*Archichauliodes*, *Ichthybotus*, *Stenoperla*, and the flatworms (Turbellaria) were clearly predators, whereas *Ameletopsis* and *Antipodochlora* are more likely to be omnivores. The predator

*Archichauliodes* had less negative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at pasture than at forest sites (Table 1, 2). Fish were clearly second-level carnivores. Among fish and crayfish there was a strong trend of increasing  $\delta^{15}\text{N}$  values from native forest to exotic forest to pasture (Table 1). Common smelt had much higher  $\delta^{15}\text{N}$  than other fish at site PT2, probably reflecting their up-stream migration from the sea and lower river to their stream spawning sites.

The mean amount of DIC was greater in pasture than in exotic forest (Table 3A; Kruskal-Wallis  $P = 0.018$ ; Tukey multiple range test  $P = 0.007$ ). However, the  $\delta^{13}\text{C}$  of the DIC was not different among land-use types (Table 3B; Kruskal-Wallis  $P = 0.068$ ), and ranged widely from  $-10.3$  to  $-19.5\text{‰}$ . Assuming that the DIC was the main source of C for aquatic photosynthesis, the mean shift in  $\delta^{13}\text{C}$  caused by photosynthesis in the epilithic diatoms was  $18.1\text{‰}$  at native forest sites ( $-14.2$  decreased to  $-32.2\text{‰}$ ),  $18.6\text{‰}$  at exotic forest sites ( $-13.0$  decreased to  $-31.6\text{‰}$ ), but only  $8.1\text{‰}$  at pasture sites ( $-16.5$  decreased to  $-24.6\text{‰}$ ). By visual examination it was found that all thin ( $<0.5$  mm) epilithic films in this study were dominated by diatoms. Filamentous green algae at pasture sites had a very wide range of  $\delta^{13}\text{C}$  values ( $-18.8$  to  $-28.9\text{‰}$ ). *Batrachospermum*, a filamentous red alga

**Table 4** Variability of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of *Cladophora* and watercress at a pasture site (PW2) in late summer (9 March 1995; S. E. Bunn unpubl. data).

Autotroph	Habitat	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Cladophora</i>	pool	-22.7	3.42
<i>Cladophora</i>	pool	-23.2	2.83
<i>Cladophora</i>	pool	-23.6	2.89
<i>Cladophora</i>	run	-27.3	3.14
<i>Cladophora</i>	run	-27.4	2.20
<i>Cladophora</i>	run	-29.7	2.57
Watercress		-27.8	4.01
Watercress		-28.3	5.02
Watercress		-28.6	4.53
Watercress		-28.9	5.52
Watercress		-29.3	5.67

**Table 5** Occurrence of aquatic and terrestrial prey items in the guts of fish in streams in native and exotic forest, and in pasture, in the Waikato region, New Zealand.

Land-use type	Total no. of fish examined	Total no. of taxa	% aquatic taxa	% terrestrial taxa
<b>Longfinned eels</b>				
Native forest	22	32	56	44
Exotic forest	28	42	62	38
Pasture	23	31	58	42
<b>Shortfinned eels</b>				
Native forest	7	7	71	29
Exotic forest	7	11	100	0
Pasture	21	27	78	22
<b>Banded kokopu</b>				
Native forest	7	19	53	47
Exotic forest	1	1	100	0
<b>Cran's bully</b>				
Exotic forest	6	9	100	0
Pasture	4	9	100	0
<b>Redfinned bully</b>				
Exotic forest	1	5	100	0
<b>Common smelt</b>				
Pasture	5	8	100	0

that was found at one exotic forest site, had a very low  $\delta^{13}\text{C}$  value ( $-40.1\text{‰}$ ; Table 1).

Localised differences in water velocity appeared to have affected the  $^{13}\text{C}$  depletion of filamentous green algae, and might account for the wide range of  $\delta^{13}\text{C}$  values that were found. *Cladophora* and *Spirogyra* were the commonly occurring genera of filamentous green algae, and formed substantial accumulations in slower flowing microsites in the pasture streams in January and February 1993. The  $\delta^{13}\text{C}$  of *Cladophora* was considerably less negative in pools (mean  $-23.2\text{‰}$ ) than in runs (mean  $-28.1\text{‰}$ ; Table 4). Pools in similar sized Waikato streams had a mean velocity of  $0.12\text{ m s}^{-1}$  ( $N = 95$ ), but at the margins, where the greatest abundance of filamentous algae occurred, water velocities were close to zero. Runs had a mean velocity of  $0.24\text{ m s}^{-1}$  ( $N = 95$ ; B. J. Hicks unpubl. data). Mean  $\delta^{15}\text{N}$  for filamentous algae was not

different among pool and run habitats, and the mean for both habitats was  $2.8\text{‰}$  (95% confidence interval =  $0.4\text{‰}$ ,  $N = 6$ ). Watercress was too  $^{13}\text{C}$ -depleted, and too  $^{15}\text{N}$ -enriched to have contributed significantly to the food webs of pasture streams (Table 4).

The gastropod scrapers *Latia* and *Potamopyrgus* collected in 1993 and 1994 had low  $\delta^{13}\text{C}$  values because they were processed with their shells, so were contaminated with non-dietary C. To test the effect of this contamination, the 1995 samples from PW2 were acid-washed to remove the  $\text{CaCO}_3$  in the shells. An acid-washed sample of *Potamopyrgus* had a  $\delta^{13}\text{C}$  of  $-25.1\text{‰}$ , compared to  $-20.1\text{‰}$  for a sample that was not acid-washed. The  $\delta^{15}\text{N}$  value was unaffected by acid washing; the acid-washed *Potamopyrgus* sample had a  $\delta^{15}\text{N}$  of  $5.0\text{‰}$ , compared to  $4.7\text{‰}$  for the sample that was not acid-washed (S. E. Bunn unpubl. data).

**Table 6** Food items in fish guts in streams in forest and pasture in the Waikato region, New Zealand. Aquatic insects are larval or nymphal stages unless otherwise stated. Only items occurring in  $\geq 10\%$  of the guts examined are listed. (Origin: t = terrestrial; a = aquatic.)

Native forest			Exotic forest			Pasture		
Item	%	Origin	Item	%	Origin	Item	%	Origin
<b>Longfinned eels</b>								
Cicada	36	t	<i>Zephlebia</i>	50	a	<i>Hydrobiosis</i>	70	a
Leptophlebiidae	36	a	Oligochaete	29	a	<i>Potamopyrgus</i>	48	a
Crayfish	32	a	Harvestman	25	t	Harvestman	35	t
Harvestman	27	t	<i>Ichthybotus</i>	25	a	Crayfish	30	a
Spider	23	t	Crayfish	25	a	Leptophlebiidae	26	a
<i>Zephlebia</i>	18	a	Millipede	25	t	Amphipod	22	a
<i>Deleatidium</i>	14	a	Cicada	21	t	<i>Aoteapsyche</i>	17	a
Gordian worm	14	a	<i>Aoteapsyche</i>	18	a	Brown beetle	13	t
Green beetle	14	t	Caterpillar	18	t	Chironomid	13	a
Oligochaete	14	a	<i>Deleatidium</i>	18	a	<i>Deleatidium</i>	13	a
			Spider	14	t			
			Ant	11	t			
			<i>Hydrobiosis</i>	11	a			
<b>Shortfinned eels</b>								
Leptophlebiidae	71	a	<i>Zephlebia</i>	57	a	<i>Hydrobiosis</i>	52	a
Crayfish	57	a	Crayfish	43	a	Chironomidae	33	a
<i>Deleatidium</i>	29	a	<i>Ichthybotus</i>	29	a	Leptophlebiidae	24	a
Ant	14	t	Oligochaete	29	a	<i>Oxyethira</i>	24	a
Beetle	14	t	<i>Ameletopsis</i>	14	a	Amphipod	14	a
<i>Polypectropus</i>	14	a	Amphipod	14	a	Cased caddis	14	a
<i>Zephlebia</i>	14	a	<i>Archichauliodes</i>	14	a	Harvestman	14	t
			Ceratopogonidae	14	a	Oligochaete	14	a
			<i>Coloburiscus</i>	14	a	<i>Potamopyrgus</i>	14	a
			<i>Deleatidium</i>	14	a	Caterpillar	10	t
			Leptophlebiidae	14	a	<i>Deleatidium</i>	10	a
						Spider	10	t
						Tipulid	10	a



**Gut contents of fish**

Out of 132 fish guts examined, only two were completely empty. It was necessary to enumerate items in the whole gut, rather than just the stomach, as the hindgut of many fish was much fuller than the stomach. Most prey items were identifiable, though because of the advanced stage of digestion, some items could be recognised only by small fragments. For this reason volumetric and mass analyses were impractical. Aquatic prey were found in all fish with any food in their gut, but terrestrial prey were also important for longfinned eels in all land-use types, and for banded kokopu (Table 5).

Terrestrial prey had a lower percentage occurrence in the guts of shortfinned eels than in longfinned eels, and were not eaten at all by Cran's bully, common smelt, or the one redfinned bully that was found.

For longfinned eels in forested streams, cicadas (*Amphisalta zelandica*) were a common food item, as were the leptophlebiid mayfly nymphs including *Zephlebia* and *Deleatidium*, and crayfish (Table 6). In exotic forest streams, oligochaetes were a common food. In pasture streams, *Hydrobiosis* and *Potamopyrgus* were the most frequent food items for longfinned eels, whereas terrestrial harvestmen

**Table 6** (continued).

Native forest			Exotic forest			Pasture		
Item	%	Origin	Item	%	Origin	Item	%	Origin
<b>Banded kokopu</b>								
Ant	86	t	<i>Deleatidium</i>	100	a			
Cicada	57	t						
<i>Zephlebia</i>	57	a						
Harvestman	43	t						
Beetle	29	t						
Hydraenid adult	29	a						
<i>Aoteapsyche</i>	14	a						
Bully	14	a						
Caddisfly	14	a						
Centipede	14	t						
<i>Deleatidium</i>	14	a						
Elmid adult	14	a						
Green beetle	14	t						
<i>Hydrobiosis</i>	14	a						
Isopod	14	t						
Leptophlebiidae	14	a						
Millipede	14	t						
<i>Potamopyrgus</i>	14	a						
Spider	14	t						
<b>Cran's bullies</b>								
			<i>Deleatidium</i>	33	a	Chironomid	100	a
			Leptophlebiidae	33	a	<i>Oxyethira</i>	75	a
			<i>Aoteapsyche</i>	17	a	<i>Candonocypris</i>	50	a
			<i>Coloburiscus</i>	17	a	<i>Hydrobiosis</i>	50	a
			Conoesucidae	17	a	<i>Austrosimulium</i>	25	a
			<i>Ichthybotus</i>	17	a	<i>Deleatidium</i>	25	a
			Polycentropidae	17	a	Dipteran	25	a
			<i>Zephlebia</i>	17	a	Empididae adult	25	a
<b>Common smelt</b>								
						<i>Oxyethira</i>	100	a
						Chironomid	60	a
						Amphipod	40	a
						Caddisfly	40	a
						Elmid adult	40	a
						<i>Deleatidium</i>	20	a
						<i>Hydrobiosis</i>	20	a
						Leptophlebiidae	20	a

(Order Opiliones) were frequent dietary items in all land-use types. For shortfinned eels, harvestmen were the only important terrestrial prey in pasture streams (Table 6). Leptophlebiid mayflies and crayfish were the most frequent prey items of shortfinned eels in forested streams, whereas *Hydrobiosis* and chironomid larvae were the most frequent prey items in pasture streams. Banded kokopu in native forest streams ate mainly ants (Family Formicidae), cicadas, *Zephlebia*, and harvestmen (Table 6). In Cran's bullies in exotic forest, *Deleatidium* and other leptophlebiid mayflies were the dominant dietary items, whereas in pasture, chironomids, the caddises *Oxyethira* and *Hydrobiosis*, and the ostracod *Candonocypris* were the principal foods. Common smelt ate mainly *Oxyethira* larvae, chironomids, amphipods, unidentified caddis larvae, and elmid beetles.

Among the less common items eaten by fish (i.e., <10% occurrence) there was a wide variety of aquatic and terrestrial taxa. Aquatic taxa were more numerous ( $N = 43$ ) than were terrestrial taxa ( $N = 23$ ). The intestinal parasite *Eustrongylodes*, or shagworm, was found in 86% of longfinned eels in native forest, 82% in exotic forest, and 74% in pasture. In shortfinned eels, shagworms occurred in 29% of eels in native forest, but not in the other land-use types. In banded kokopu, shagworms occurred in one out of the seven fish found in native forest, but not in the one fish found in exotic forest. There was no difference in  $\delta^{13}\text{C}$  between fish that had a large proportion of terrestrial taxa ( $\geq 40\%$  of food items) and those that had none in their stomachs when sampled (Mann-Whitney  $U$  test;  $P = 0.390$ ).

## DISCUSSION

### Stable isotope ratios and food web analysis

Food webs in these forested Waikato streams were based on allochthonous material. Epilithic diatoms appeared to be unimportant C sources for all invertebrates except for the  $^{13}\text{C}$ -depleted collector-browser *Nesameletus*. At some stream sites on the West Coast, South Island, *Nesameletus* was similarly  $^{13}\text{C}$ -depleted (Winterbourn et al. 1984). Patterns of isotopic fractionation among the food-web components were consistent with the highly shaded nature of the forested sites, where photosynthesis was limited, epilithon biomass was low (Quinn et al. 1997a), and the riparian trees ensured a supply of allochthonous material.

Food webs in the open, pasture streams in this study were more  $^{13}\text{C}$ -enriched than were the shaded, forested streams, contrary to some previous New Zealand studies in which food webs at open sites were more  $^{13}\text{C}$ -depleted than at shaded sites (Rounick et al. 1982; Winterbourn et al. 1984). Food-web  $^{13}\text{C}$ -enrichment in Waikato streams seems to be attributable to the autotrophs. Epilithic diatoms were significantly more  $^{13}\text{C}$ -enriched at pasture sites than at forested sites (Table 1), in contrast to Wellington streams where stone surface scrapings at open sites were highly  $^{13}\text{C}$ -depleted ( $-34.3$  to  $-35.8\%$ ; Rounick & Hicks 1985). Though  $^{13}\text{C}$ -enriched food webs occurred in Wellington streams, this enrichment at both open and shaded sites was based on the  $^{13}\text{C}$ -enrichment of fine particulate organic matter rather than epilithon (Rounick & Hicks 1985). However, at open, pasture sites in the Waikato, the epilithic diatoms themselves were  $^{13}\text{C}$ -enriched compared to shaded, forest sites.

The wide range of  $\delta^{13}\text{C}$  and  $^{15}\text{N}$  values for the autotrophs in pasture streams made the extent of their contribution to food webs difficult to assess. The high rates of photosynthesis at these unshaded sites, combined with high temperatures (Quinn et al. 1997a), suggest that autotrophic production was responsible for the high eel biomass and productivity found by Hicks & McCaughan (1997). The present study lacked a truly representative sampling of autotrophs that might have shown the quantitative contribution of primary producers to the pasture stream food webs. Also, microsite water velocity influenced the  $\delta^{13}\text{C}$  value of filamentous green algae in the 1995 sampling (Table 4). Water velocity was not recorded in the original 1993/94 sampling. The link between high rates of photosynthesis, low water velocities, and  $^{13}\text{C}$ -enrichment of aquatic autotrophs requires further investigation.

The dual isotope plot suggests that allochthonous material also contributed to the food webs in pasture streams (Fig. 1). The  $^{13}\text{C}$ -enrichment of conditioned leaf litter in pasture streams compared to forested streams (Table 1) may have been caused by diatoms growing on submerged leaf surfaces. In pasture streams, the invertebrates *Deleatidium*, *Nesameletus*, and the hypsychid caddises also showed  $^{13}\text{C}$ -enrichment, consistent the  $\delta^{13}\text{C}$  of the potential foods epilithic diatoms and FPOM derived from conditioned leaf litter. The  $^{13}\text{C}$ -enrichment of *Archichauliodes* suggested that it preyed primarily on some or all of these invertebrate taxa.

Filamentous green algae appear to have been unavailable to invertebrates other than *Potamopyrgus* and crayfish; Bunn et al. (1997) similarly concluded that *Spirogyra* in a tropical stream had limited availability to invertebrate consumers. Watercress was also not a significant C source in the pasture streams in which it occurred.

Fish in the Waikato had similar  $\delta^{13}\text{C}$  values in all land-use types (means  $-23.9$  to  $-25.6\text{‰}$ ). This homogeneity may have resulted partly from the relatively large sample size ( $N = 129$ ) in this study compared to previous studies. Fish in streams in the Wellington region had  $\delta^{13}\text{C}$  values between  $-19.5$  and  $-24.9\text{‰}$  in a mixture of open and shaded sites (Rounick & Hicks 1985). In streams under native forest on the West Coast of New Zealand, banded kokopu had  $\delta^{13}\text{C}$  values between  $-22$  and  $-25\text{‰}$  (Main & Lyon 1988).

Terrestrial taxa were significant in the diet of longfinned eels and banded kokopu in the Waikato, but the diets of shortfinned eels, Cran's bullies, and common smelt were dominated by aquatic taxa (Table 5). Main & Lyon (1988) also reported that banded kokopu ate terrestrial prey. In the Waikato, fish feeding to a large extent ( $\geq 40\%$ ) on terrestrial prey could not be distinguished isotopically from fish that ate exclusively aquatic prey. Terrestrial invertebrates as a C source might have confused the food web analysis, particularly since the isotopic ratios of terrestrial taxa were not measured in this study. Main & Lyon found that the  $\delta^{13}\text{C}$  of terrestrial invertebrates ranged from  $-21$  to  $-28\text{‰}$ , with most values close to  $-25\text{‰}$ . Another New Zealand study found that the  $\delta^{13}\text{C}$  for terrestrial invertebrates was  $-24.4 \pm 1.4\text{‰}$  (mean  $\pm 95\%$  confidence interval;  $N = 10$ ; McDowall et al. 1996). Without corresponding  $\delta^{15}\text{N}$  values, these values cannot be distinguished from those of aquatic invertebrates.

*Potamopyrgus* appears to have eaten filamentous green algae. The 1995 mean  $\delta^{13}\text{C}$  of filamentous green algae in runs ( $-28.1\text{‰}$ ) and its mean  $\delta^{15}\text{N}$  ( $2.8\text{‰}$ ) suggest that it could have been a food for *Potamopyrgus* (acid-washed  $\delta^{13}\text{C} = -25.1\text{‰}$  and  $\delta^{15}\text{N} = 5.0\text{‰}$ ). Further sampling is required to improve our knowledge of the relationship between molluscs and filamentous algae. The contamination of the *Potamopyrgus* samples by non-dietary C (e.g., Tanaka et al. 1986) has been confirmed in this study, and should be avoided in future.

Crayfish in Waikato streams appear from their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values to be primarily predators, deriving most of their C from invertebrates. Though

detritivory has been demonstrated in New Zealand crayfish (Parkyn et al. 1997), assimilation rates of plant material are likely to be low. In streams in Missouri, United States, the crayfish *Orconectes* assimilated only 14% of its detrital food compared to 92% of invertebrate food. These crayfish also ate filamentous algae, with an assimilation efficiency of 39% (Whitledge 1996). The assimilation efficiency of *Paranephrops zealandicus* for fresh and decayed oxygen weed (*Elodea canadensis*) averaged 21% (Musgrove 1988). Crayfish in the present study (mean  $\delta^{13}\text{C} -24.4$  to  $-24.5\text{‰}$ ) were the most  $^{13}\text{C}$ -enriched of any consumer except for the gastropod scrapers, whose analyses were contaminated with non-dietary carbonates. Main & Lyon (1988) also found that *P. planifrons* was the most highly  $^{13}\text{C}$ -enriched invertebrate ( $-24.6\text{‰}$ ) in streams in South Westland, New Zealand. One explanation for the  $^{13}\text{C}$ -enrichment is that food in the crayfish gut might be assimilated by micro-organisms, with subsequent assimilation of these micro-organisms by the crayfish. Cellulase activity, which is normally absent from higher eukaryote organisms, has been detected in the gut of *P. zealandicus* (Musgrove 1988). This activity was associated with bacteria in the gut, but the extent of the contribution to crayfish nutrition by these micro-organisms was not established, and thus the expected isotopic enrichment is unknown. Filamentous green algae are a possible food source of crayfish in pasture streams in the Waikato, as the fractionation of C and N isotopes is in the right direction, and of about the right magnitude. In forested streams, where filamentous algae were generally absent, the  $\delta^{13}\text{C}$ -enrichment of crayfish suggests that their predominant food was invertebrates.

Analyses of  $\delta^{15}\text{N}$  augmented the  $\delta^{13}\text{C}$  analyses in this study, providing a second dimension that was useful for resolving trophic links. The use of both C and N isotopes overcame some of the criticisms recently aimed at stable C isotope studies by France (1995a; 1996a,b,c). There was a progressive enrichment in  $\delta^{15}\text{N}$  in equivalent trophic levels between native forest and exotic forest, and between exotic forest and pasture. Invertebrates, eels, and crayfish in pasture streams were 2–3‰ greater in  $\delta^{15}\text{N}$  than they were in native forest streams (Table 1). Contributions of ruminant excreta or nitrogenous fertilisers to ground water might have caused the  $^{15}\text{N}$ -enrichment of pasture streams. The exotic forest sites were in pasture until c. 15 years ago, which might account for their intermediate

$^{15}\text{N}$ -enrichment. The difference in  $\delta^{15}\text{N}$  values between leaf litter and top consumers in this study (7.0–8.4‰) was similar to forested streams in the Pacific northwest of the United States (Fry 1991), though top consumers were considerably more enriched in  $^{13}\text{C}$  in the United States' studies. The average size of trophic steps was 2–3‰ for  $\delta^{15}\text{N}$ , and 0.7–1.6‰ for  $\delta^{13}\text{C}$ , close to expected values (Rounick & Hicks 1985; Peterson & Fry 1987; Handley & Raven 1992). The  $\delta^{15}\text{N}$  of the migratory common smelt (12.3‰) was twice that of any other fish species, possibly reflecting consumption of  $^{15}\text{N}$ -enriched estuarine or marine plankton (Peterson & Howarth 1987).

### Variability of autotrophic $\delta^{13}\text{C}$

Variability in DIC did not appear to account for the variable  $\delta^{13}\text{C}$  of the autotrophs in this study. DIC  $\delta^{13}\text{C}$  means (–13.0 to –16.5‰) were similar in all land uses, and were also similar to the range previously reported in New Zealand streams (–11.1 to –15.5‰; Rounick et al. 1982; Rounick & Hicks 1985). In forested Waikato streams, epilithic diatoms (mean  $\delta^{13}\text{C}$  c. –32‰) were 18–19‰ more negative than the DIC, similar to predicted  $^{13}\text{C}$ -depletion by photosynthesis. At pasture sites, assuming that DIC was the C source for photosynthesis, epilithic diatoms were only c. 8‰ more negative than the DIC.  $^{13}\text{C}$ -enriched periphyton have been found at other stream sites in New Zealand;  $\delta^{13}\text{C}$  values of –10 to –15‰ were found at open sites in the Styx River (Lester et al. 1995). Filamentous algae from open sites in the Manganuiateao River, central North Island, also had  $^{13}\text{C}$ -enriched values ( $\delta^{13}\text{C}$  –12.5 to –16.8‰; Collier & Lyon 1991).

One mechanism by which autotrophs can become  $^{13}\text{C}$ -enriched is through C limitation of photosynthesis, as competition for C substrate causes the usual discrimination against  $^{13}\text{C}$  to break down. Low water velocity can cause increases in autotrophic  $\delta^{13}\text{C}$  through restricted mixing. Though substrate limitation of photosynthesis is unexpected in a well-mixed, temperate, lotic system, algae and cyanobacteria with  $^{13}\text{C}$ -enriched signatures are common in lentic environments (McCabe 1985; Bunn & Boon 1993; Boon et al. 1994). Substrate limitation in lakes can result in phytoplankton with  $\delta^{13}\text{C}$  values close to 0‰ (McCabe 1985). In streams with high algal biomass, C limitation of photosynthesis might be sufficient to cause  $^{13}\text{C}$  enrichment of the algae at low-velocity microsites.

Biomass of epilithon, including filamentous algae, was higher at pasture sites than at forested sites (Quinn et al. 1997a). The mean values at pasture sites in November (3.6 g AFDM  $\text{m}^{-2}$ ) were not high compared to previously recorded values in New Zealand streams, and to values recorded in unshaded channels at a pasture site in summer (maximum 12 g C  $\text{m}^{-2}$ , = c. 24 g AFDM  $\text{m}^{-2}$ ; Quinn et al. 1997b). *Cladophora*-dominated algal communities can have biomasses in excess of 100 g AFDM  $\text{m}^{-2}$  (Biggs & Price 1987). However, in midsummer at my sites, substantial abundance of filamentous green algae was observed. Algal accumulation depends on the length of period of flow recession as well as on nutrient status of the water (Biggs 1995). Maximum accumulation would be expected to occur around midsummer, when the samples for this study were taken, rather than in November when Quinn et al. (1997a) sampled.

Thus it is conceivable that in summer at microsites with high temperature, high accumulation of algal biomass, and low water velocity, the C substrate for photosynthesis might become limiting in streams. Variable  $\delta^{13}\text{C}$  values in autotrophs could have resulted from sampling a variety of microhabitats with different water velocities. Alternatively, microbial respiration under low velocity conditions might have resulted in an undiscovered pool of dissolved inorganic carbon that was used by the autotrophs in Waikato streams.

### CONCLUSIONS

Stable C and N isotope analyses combined with fish gut analyses have helped elucidate the structure of food webs in Waikato streams under different land uses. Within each of the three land uses, stream ecosystems behaved consistently. The food webs in forested streams followed the conventional small-stream, allochthonous-dominated model, whereas food webs in pasture streams had a mixture of allochthonous and  $^{13}\text{C}$ -enriched autochthonous inputs. For pasture streams, key areas for more detailed analysis are suggested. Questions remaining after this study include: (1) the cause of the variability in  $\delta^{13}\text{C}$  of the autotrophs, including seasonal variation; (2) the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of the contributing ground waters, and the extent to which the stream food web reflects these; (3) the role of dissolved organic carbon in stream food webs; and (4) the quantitative importance of terrestrial invertebrates. To improve our

understanding of stream food webs through analysis of stable C and N isotopes, more attention to the C and N dynamics of epilithic films, and to their relation to groundwater inputs is necessary.

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