Stable isotope analysis of nutrient pathways leading to Atlantic salmon[1]

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Abstract: The relative contribution of terrestrial and aquatic primary energy sources in food webs along a stream continuum in the Miramichi River system, New Brunswick, was investigated through the use of stable carbon and nitrogen isotope ratios. In sites where these primary energy sources were isotopically distinct, quantitative mixing models were used to identify the relative importance of allochthonous carbon in the diets of wild juvenile Atlantic salmon (*Salmo salar*) and other resident stream fishes. The $\delta^{13}C$ data of the stream fauna ranged from –34‰ to –20‰, suggesting variable assimilation of allochthonous and autochthonous carbon sources at the four study sites. Results from the mixing model were congruent with the stream continuum hypothesis, indicating that fishes in the headwaters of Catamaran Brook were more dependent (>85%) on allochthonous carbon sources than those in sites located downstream (36–52%). Stable nitrogen isotope distributions successfully described food web structure in this study, suggesting at least 2.5–3.5 trophic levels in these lotic ecosystems. Stable isotope ratios of carbon were particularly useful for illustrating seasonal changes in food resources of recently emerged age 0+ salmon as maternally derived marine carbon was subsequently diluted by freshwater carbon over the growing season.

Résumé : Pour étudier la contribution relative des sources d'énergie primaire dans des réseaux trophiques aquatiques et terrestres du continuum d'un cours d'eau du réseau hydrographique de la rivière Miramichi, au Nouveau-Brunswick, on a mesuré les rapports d'isotopes stables du carbone et de l'azote. Pour les lieux où les sources d'énergie primaire se distinguaient par leur profil isotopique, on a utilisé des modèles de mélange quantitatifs pour déterminer l'importance relative du carbone allochtone dans l'alimentation du saumon de l'Atlantique (*Salmo salar*) juvénile sauvage et d'autres poissons vivant dans le cours d'eau. Les valeurs de $\delta^{13}C$ mesurées chez la faune du cours d'eau allaient de –34‰ à –20‰, ce qui laisse entrevoir une assimilation variable du carbone allochtone et du carbone autochtone dans les quatre lieux étudiés. Les résultats obtenus au moyen du modèle de mélange sont compatibles avec l'hypothèse du continuum, ce qui signifie que les poissons du cours supérieur du ruisseau Catamaran dépendent davantage (>85%) des sources de carbone allochtone que les poissons des parties plus en aval du cours d'eau (36–52%). Les distributions d'isotopes de l'azote stables donnent une idée représentative, dans le contexte de cette étude, de la structure des réseaux trophiques et indiquent qu'il y aurait 2,5–3,5 niveaux trophiques dans ces écosystèmes lotiques. Les rapports entre les isotopes stables du carbone sont particulièrement utiles pour décrire les changements saisonniers des ressources alimentaires des saumons d'âge 0+ d'éclosion récente car, durant la saison de croissance, le carbone maternel provenant du milieu marin est diluée par le carbone provenant des eaux douces.
[Traduit par la Rédaction]

Introduction

According to Vannote et al. (1980), stream food webs are based on a gradient of terrestrial (i.e., allochthonous) and aquatic (i.e., autochthonous) primary energy sources from headwaters to river mouth. However, the actual dependence of aquatic communities on these energy sources has rarely been measured and is not always clear (Bird and Kaushik 1984). Stable isotope analysis (SIA) is one way to assess the relative importance of allochthonous and autochthonous inputs in streams. Initially used by earth scientists to track the geochemical cycling of elements, the SIA technique is now finding wide application in the biological sciences where carbon, nitrogen, and sulfur have proved most useful in analyzing food web relations (see reviews by Fry and Sherr 1984; Peterson and Fry 1987; Rundel et al. 1989; Lajtha and Michener 1994). Stable isotopes of carbon, ^{13}C and ^{12}C, have been used most often (Rounick and Winterbourn 1986). Their ratios allow the identification of important primary food sources because they are fixed during photosynthesis and are passed along food chains relatively unchanged (DeNiro and Epstein 1978).

Freshwater streams provide favourable conditions for tracing carbon pathways, as terrestrial and aquatic plants often differ in their stable isotopic compositions (Rau 1980; Rounick et al. 1982). Carbon fixed by terrestrial C_3 plants in temperate regions has a characteristic $^{13}C/^{12}C$ ratio (expressed as $\delta^{13}C$, a parts per thousand difference from a standard reference material) of approximately –28‰ (O'Leary 1988). Aquatic plants exhibit a much wider range in $\delta^{13}C$ (–50‰ to –10‰) relative to terrestrial plants, reflecting site-specific

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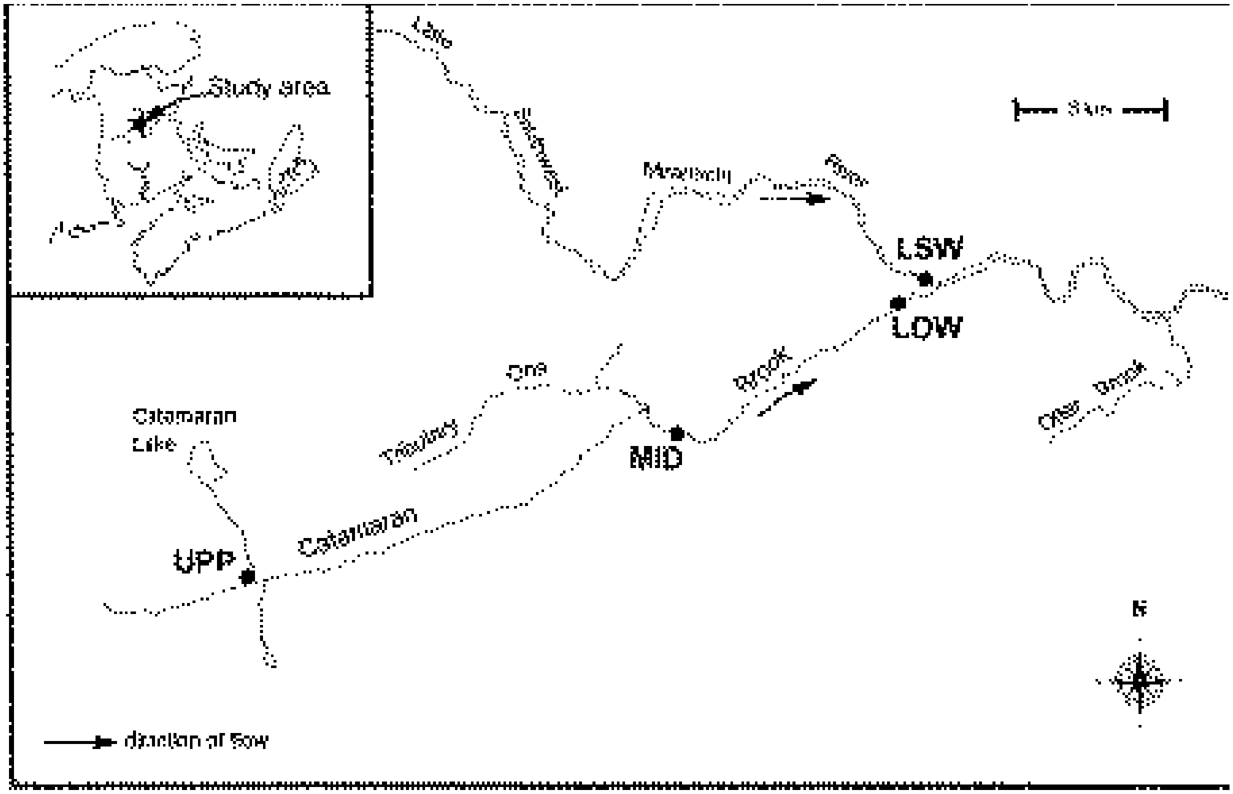
Fig. 1. Map of the study area in New Brunswick, eastern Canada, showing sampling locations in Catamaran Brook (UPP, MID, and LOW) and in the Little Southwest Miramichi River (LSW).



and species-specific factors (Osmond et al. 1981; Farquhar et al. 1989). Recent studies using SIA in the investigation of stream food webs include Bunn et al. (1989), Hesslein et al. (1991), Rosenfeld and Roff (1992), Forsberg et al. (1993), and references therein. Most studies tend to be qualitative; only Junger and Planas (1994) made an attempt to quantify the relative importance of terrestrial and aquatic carbon sources to the stream food web.

We used SIA in an attempt to determine the important primary sources of organic carbon utilized by wild juvenile Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. To our knowledge, juvenile Atlantic salmon have not been previously considered in quantitative descriptions of allochthonous–autochthonous carbon dependence (Waters 1993); nor has any prior investigation reported on the stable isotopic composition of food webs in salmon streams of Atlantic Canada. To do this, we measured $^{13}C/^{12}C$ ratios in fish, benthic invertebrates, and terrestrial and aquatic plants. In sites where terrestrial and aquatic plants were shown to be isotopically distinct, quantitative isotopic mixing models (Fry and Sherr 1984) were applied to measure the relative contribution of allochthonous carbon to the fish community. We also analyzed the $^{15}N/^{14}N$ ratios of plants and animals, as an added descriptor of stream food web structure. Nitrogen isotope ratios are enriched by ≈3‰ at each level in the food chain (Minagawa and Wada 1984), thus making them useful indicators of trophic status. Because Catamaran Brook is the site of a long-term scientific study designed to monitor the effects of forestry practices on Atlantic salmon and their instream habitats (Cunjak et al. 1990), a subsidiary aim of our work was to provide baseline stable isotope data against which post-deforestation conditions could be judged. SIA has been used successfully to demonstrate some effects of clearcutting in some New Zealand catchments several years after logging (Rounick et al. 1982; Winterbourn and Rounick 1985; Rounick and Winterbourn 1986).

Methods

Study area

Samples for SIA were collected during 1992 and 1993 in Catamaran Brook (46°52.7′N, 66°06.0′W), a third-order stream in central New Brunswick. Major collection dates included 18–27 May, 2–9 July, 14–19 August, and 8–15 October. Three sites were selected at approximately 18 km (UPP), 8 km (MID), and 1 km (LOW) upstream of the mouth of Catamaran Brook (Fig. 1). An additional site was chosen at the Little Southwest Miramichi River (LSW) about 50 m upstream of the confluence with Catamaran Brook. Morphometric and environmental variables characterizing the study sites are presented in Table 1. A comprehensive description of the physical, chemical, and biological conditions of the brook and its drainage basin is provided in Cunjak et al. (1993).

Collection and preparation of samples

To determine the isotopic signature of the allochthonous carbon source, leaf litter samples were hand-picked from the lower reach of Catamaran Brook (LOW) and sorted to represent common riparian tree species. For site-specific autochthonous carbon labels, the filamentous chlorophyte, *Cladophora* sp., was used because it was available in sufficient quantity at all sites and to avoid the previously reported difficulty of separating terrestrially derived detritus from algae in rock scrapings (Winterbourn et al. 1984; Rounick and Hicks

Table 1. Environmental and morphometric characteristics of the four study sites during the 1992–1993 sampling period.

	Upper Reach (UPP)	Catamaran Brook Middle Reach (MID)	Lower Reach (LOW)	Little Southwest Miramichi River (LSW)
Catchment area (km^2)	12	25	52	1200
Altitude (m)	250	155	75	70
Slope (%)	3.6	1.1	0.6	0.4
Width (m)	3.9	6.9	9.3	90
Mean depth (m)*	0.26	0.28	0.40	0.68
Mean velocity (m·s^{-1})*	0.10	0.35	0.32	0.76
Discharge (m^3·s^{-1})*	0.07	0.68	1.20	17.4
Temperature (°C)*	19	17	20	23
pH*	7.5	7.1	7.0	6.9
Conductivity (µS·cm^{-1})*	59	48	44	25

*Values are means measured during the 1992–1993 sampling period.

1985; Junger and Planas 1994). Other aquatic plants, *Potamogeton* sp. and *Fontinalis* sp., were also collected for determination of their site-specific isotopic signatures. Stream water was sampled at each site for dissolved inorganic carbon (DIC) δ^{13}C values. Each water sample was sealed in airtight 500-mL glass bottles, preserved with 1 mL of mercuric chloride ($HgCl_2$) solution, and refrigerated until isotope analysis was performed.

Aquatic invertebrates representing major functional feeding groups were identified and used in the analysis: scraper–grazers, *Glossosoma* (Trichoptera: Glossosomatidae) and *Ephemerella* (Ephemeroptera: Ephemerellidae); shredder, *Pteronarcys* (Plecoptera: Pteronarcidae); collector-filterers, *Simulium* (Diptera: Simuliidae) and *Hydropsyche* (Trichoptera: Hydropsychidae); and predator, *Isogenoides* (Plecoptera: Perlodidae). Each sample consisted of enough individuals (up to 10) to provide the minimum of 10 mg (dry weight) needed for isotope analysis. Sections of muscle tissue from behind the dorsal fin and above the lateral line were collected from age 0+ (fork length (FL) 3–5 cm), age 1+ (FL 6–9 cm), and age 2+ Atlantic salmon (FL 10–13 cm), brook trout (*Salvelinus fontinalis*) (FL 8–18 cm), and blacknose dace (*Rhinichthys atratulus*) (FL 5–8 cm).

All samples of plant and animal material were frozen in the field and then freeze-dried in the laboratory. After drying, samples were ground to a powder, and stored in small, airtight, precombusted, glass vials prior to isotope analysis.

Isotope analysis

For SIA, organic materials were converted to gas in either sealed Pyrex (for CO_2) or quartz (for N_2) tubes following the combustion methods described by Boutton et al. (1983) for carbon, and Kendall and Grim (1990) for nitrogen. Extraction of CO_2 from stream water was accomplished by cryogenic separation in an evacuated, closed-line system, following mixture with 2 mL phosphoric acid (H_3PO_4). Analyses were done in the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ont.) using a VG Micromass 903E triple-collector isotope-ratio mass spectrometer. Isotope ratios are expressed as parts per thousand, or "per mil," differences (‰) from a standard reference material:

$$\delta X = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}\right) \times 1000$$

where X is ^{13}C or ^{15}N, R is the corresponding ratio, ^{13}C/^{12}C or ^{15}N/^{14}N, and δ is the measure of the ratio of heavy to light isotopes in a sample. Positive, or less negative, δ values denote "enrichment" or increases in the amount of the heavy isotope components. Conversely, decreases in the amount of the heavy isotope indicate "depletion." Standard reference materials, set at arbitrary values of 0‰, are carbon in the Pee Dee limestone formation (Craig 1957) and nitrogen gas in the atmosphere (Mariotti 1983). Precision for the analyses was better than ±0.2‰ for carbon and ±0.5‰ for nitrogen.

Table 2. Stable carbon isotope ratios (δ^{13}C) of decomposing leaf litter from eight of the most common riparian tree species in the Catamaran Brook basin.

Species	δ^{13}C (‰)
American beech (*Fagus grandifoila*)	–28.6
Speckled alder (*Alnus rugosa*)	–29.5
White birch (*Betula papyrifera*)	–29.5
Yellow birch (*Betula lutea*)	–29.6
Sugar maple (*Acer saccharum*)	–29.8
Red spruce (*Picea glauca*)	–30.6
Balsam fir (*Abies balsamea*)	–30.8
Eastern white cedar (*Thuja occidentalis*)	–31.5

Note: Values are means of duplicate samples collected from LOW in May, 1992.

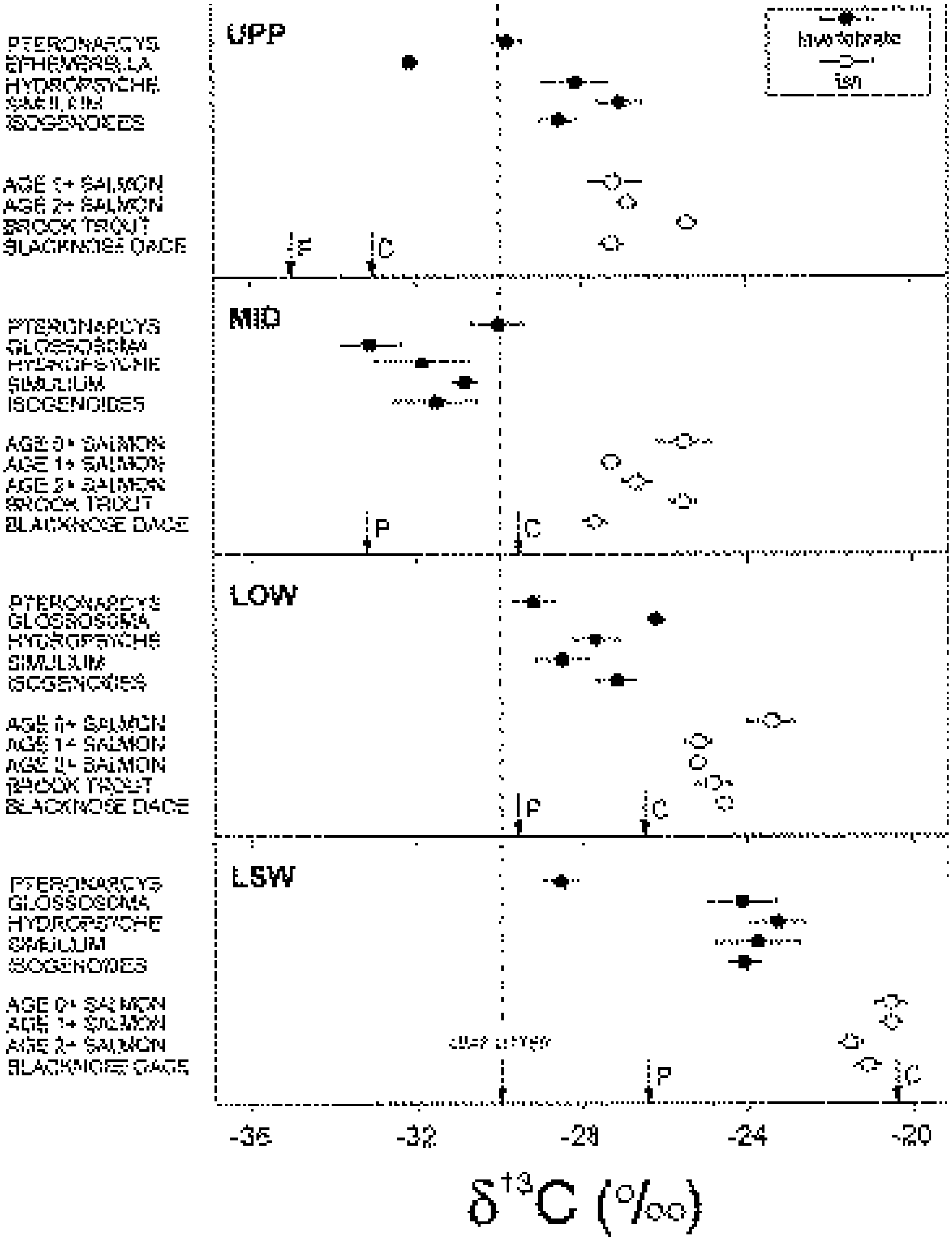
Isotopic mixing model

Because allochthonous carbon can contribute to stream food webs in more than one way (e.g., it may be consumed directly by stream herbivores, in which case it can be considered allochthonous production, or it may be respired to CO_2 and form part of autochthonous production before being utilized by herbivores), we have defined allochthonous carbon in this study as allochthonous production and report the relative importance of this carbon source (e.g., terrestrial leaf litter) to fish at each site using the following equation (modified from Junger and Planas 1994):

$$\%\ \text{allochthonous} = \left(\frac{\delta^{13}C_{\text{fish}} - \delta^{13}C_{\text{autochthonous}} - fx}{\delta^{13}C_{\text{allochthonous}} - \delta^{13}C_{\text{autochthonous}}}\right) \times 100$$

where f is the average trophic enrichment of ^{13}C between an animal

Fig. 2. Stable carbon isotope ratios (δ^{13}C) of invertebrates and fish at four study sites along a stream continuum in the Miramichi River system during the 1992–1993 sampling season (mean ± SE). Arrows refer to site-specific aquatic plant δ^{13}C values. The vertical broken line represents the average terrestrial leaf litter δ^{13}C value. C, *Cladophora*; F, *Fontinalis*; P, *Potamogeton*.



and its food (≈1‰; DeNiro and Epstein 1978), and x is the trophic position of the animal (to be determined for each fish species and age-class of salmon using the δ^{15}N data obtained in this study). $\delta^{13}C_{\mathrm{allochthonous}}$ is the average stable carbon isotope ratio of the sampled leaf litter, which was considered constant at all sites. $\delta^{13}C_{\mathrm{autochthonous}}$ is the site-specific average stable carbon isotope ratio of the algae, *Cladophora*, which was presumed to be representative of the algal carbon signature at each site. This two-source mixing model assumes that leaf litter and algae are the two most important food sources in Catamaran Brook. This hypothesis is based on the general acceptance that mosses and macrophytes are not often used as food by stream consumers (Hynes 1970).

Results

δ^{13}C of primary food sources

Decomposing leaves from eight of the most common riparian tree species in the Catamaran Brook basin had an average δ^{13}C of –30.0 ± 0.3‰ (mean ± SE), with conifer needles being slightly more depleted than deciduous leaves (Table 2). *Cladophora* had δ^{13}C values that varied across the four study sites (range –33.0‰ to –20.3‰) and were strongly correlated with those of DIC (Pearson's $r = 0.95$, $p < 0.0001$), showing a significant trend towards ^{13}C-enrichment in sites located

Table 3. Stable carbon isotope ratios (δ^{13}C) of aquatic plants and dissolved inorganic carbon (DIC) at four sites in the Miramichi River system collected during the 1992–1993 sampling period.

	UPP	MID	LOW	LSW
Dissolved inorganic carbon (DIC)	–13.3 (0.3)	–11.7 (0.1)	–10.5 (0.2)	–8.1 (0.1)
Algae (*Cladophora* sp.)	–33.0 (0.2)	–29.5 (0.2)	–26.6 (0.3)	–20.3 (0.7)
Macrophyte (*Potamogeton* sp.)	np	–32.7 (0.3)	–29.5 (0.3)	–26.7 (0.4)
Moss (*Fontinalis* sp.)	–35.6 (0.3)	np	np	np

Note: Values are means (with SE given in parentheses; $n = 3$). Abbreviations are as in Figure 1.

Table 4. Seasonality of stable carbon isotope ratios (δ^{13}C) of fish collected from four sites in the Miramichi River system collected over the 1992–1993 sampling period.

		δ^{13}C (‰)				
Site	Date	Age 0+ salmon	Age 1+ salmon	Age 2+ salmon	Brook trout	Blacknose dace
UPP	May	np	–28.1 (—) 1	–26.8 (0.4) 4	–25.2 (0.5) 4	–27.6 (—) 2
	July	np	–27.8 (0.4) 3	–27.0 (0.4) 4	–25.7 (0.3) 5	–26.9 (—) 2
	Aug.	np	–25.8 (—) 2	–26.7 (0.3) 4	–25.2 (0.1) 3	–27.2 (—) 2
MID	May	np	–27.0 (—) 2	–27.9 (0.8) 4	–25.5 (—) 2	–27.5 (—) 2
	July	–21.8 (0.8) 6	–27.6 (0.4) 7	–26.4 (0.4) 9	–26.6 (0.5) 4	–26.8 (—) 2
	Aug.	–27.0 (0.3) 12	–26.9 (0.2) 5	–26.1 (0.8) 5	–25.1 (0.4) 10	–28.0 (—) 8
	Oct.	–27.8 (–) 2	np	–26.8 (—) 2	np np	
LOW	May	np	–26.5 (—) 2	–25.9 (0.7) 4	–24.6 (0.6) 4	–24.9 (—) 2
	July	–20.0 (0.2) 6	–25.5 (0.4) 6	–25.4 (0.3) 6	–24.4 (0.8) 5	–24.4 (0.4) 4
	Aug.	–24.6 (0.4) 12	–23.9 (0.4) 6	–24.9 (0.2) 8	–25.4 (1.0) 7	–24.1 (0.5) 6
	Oct.	–26.5 (–) 2	np	–24.7 (—) 2	np	np
LSW	May	np	np	–20.9 (—) 2	np	np
	July	–20.3 (0.5) 6	–20.7 (0.3) 3	–21.5 (0.2) 9	np	–20.5 (0.1) 3
	Aug.	–21.0 (0.5) 6	–20.4 (0.2) 3	–21.7 (0.4) 7	np	–21.7 (0.3) 3
	Oct.	–21.4 (–) 2	np	–21.7 (—) 2	np	np

Note: Values are means (with SE given in parentheses) and sample sizes. np, not present at the site. Abbreviations are as in Figure 1.

downstream (Table 3). Leaf litter was isotopically distinct from *Cladophora* at all sites (Dunnett's test, $p < 0.05$) except MID ($p = 0.44$), where δ^{13}C values differed by only $\approx$0.5‰. *Potamogeton* was always more depleted than *Cladophora* and followed a similar downstream enrichment pattern (Table 3). *Fontinalis* was found only at UPP and was also more depleted than *Cladophora* (Table 3).

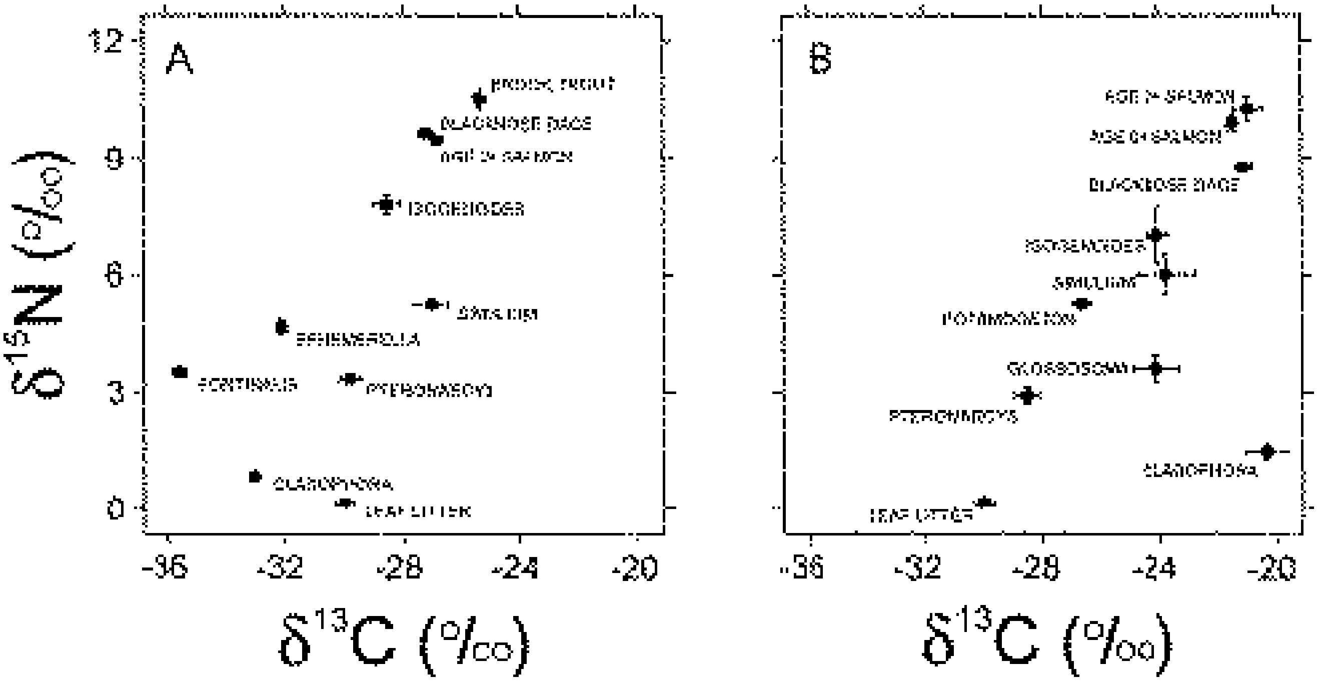
δ^{13}C of invertebrates and fish

In general, invertebrate δ^{13}C values in the headwaters of Catamaran Brook (UPP) were more similar to the δ^{13}C values of terrestrial leaves than to those of aquatic plants (Fig. 2). *Pteronarcys* had a δ^{13}C value (–29.8‰) close to that of its leaf litter diet, while *Hydropsyche* and *Simulium* were slightly more enriched at –28.1‰ and –27.0‰, respectively. *Ephemerella* was the only taxon to show a distinct algal carbon label at –32.1‰, while *Isogenoides*, possessed an intermediate δ^{13}C value (–28.6‰), consistent with its carnivorous diet on other invertebrates. Fish δ^{13}C values (range –28.1‰ to –25.2‰) were similar to, though slightly more enriched than, those of the invertebrate community (Fig. 2). Variability in fish δ^{13}C was low over the sampling season (Table 4), and brook trout were significantly more enriched than other fishes at this site (Tukey's HSD, $p < 0.01$).

Invertebrates in the middle reach of Catamaran Brook appeared to be less dependent on terrestrial carbon than those collected in the headwaters. At MID, the sampled invertebrate taxa were generally more ^{13}C-depleted (range –33.1‰ to –30.0‰) than leaf litter inputs (Fig. 2). Fish were $\approx$3–5‰ more enriched than the sampled benthos (Fig. 2). This was a surprising result because animals are typically only $\approx$1‰ more enriched than their food (DeNiro and Epstein 1978). Seasonality in fish δ^{13}C was generally low (Table 4), but recently emerged age 0+ salmon (July) were $\approx$6‰ more enriched than those sampled later in the season. Once again, brook trout were significantly more enriched (–25.5‰) than other fishes (Tukey's HSD, $p < 0.05$) except age 0+ salmon ($p = 0.96$).

Invertebrates collected from the lower reach of Catamaran Brook (LOW) were more enriched than those at MID (Fig. 2). These taxa had δ^{13}C values (range –29.2‰ to –26.2‰) located between those of terrestrial and aquatic plants, which suggested utilization of both food resources. Fish were also more ^{13}C-enriched (range –25.2‰ to –24.5‰) than those sampled upstream (Fig. 2). Recently emerged age 0+ salmon

Fig. 3. Carbon ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) profiles of plants, invertebrates, and fish collected from (A) the headwaters of Catamaran Brook (UPP) and (B) the Little Southwest Miramichi River (LSW) during the 1992–1993 sampling season. Values are means ± SE.



(July) had much higher $\delta^{13}C$ values than did other fishes (Tukey's HSD, $p < 0.05$) but showed progressive ^{13}C-depletion over the sampling season (Table 4).

Invertebrates and fish from the Little Southwest Miramichi River (LSW) site had the most enriched $\delta^{13}C$ values in this study (Fig. 2). Aside from the distinctly terrestrial label of *Pteronarcys* (–28.5‰), other taxa were less negative (range –24.1‰ to –23.8‰), suggesting greater reliance on aquatic primary production at this site. Fish $\delta^{13}C$ values were also quite high at ≈–21‰ (Fig. 2), and showed a strong dependence on aquatic carbon sources as well. Seasonal differences in fish $\delta^{13}C$ values were not strong, and age 0+ salmon $\delta^{13}C$ values decreased only slightly from July to October (Table 4).

$\delta^{15}N$ profiles

Nitrogen isotopic compositions of plants and animals collected at UPP and LSW are presented in Fig. 3. Leaf litter had the lowest $\delta^{15}N$ value at 0.2‰, while *Cladophora* was slightly higher at 1.5‰. *Potamogeton* and *Fontinalis* were ≈2–3‰ more enriched than *Cladophora*. Animal $\delta^{15}N$ generally increased at successive trophic levels. Primary consumers, such as *Pteronarcys*, *Ephemerella*, and *Glossosoma*, had $\delta^{15}N$ values that ranged from 2.9 to 4.5‰, while *Simulium* was slightly more enriched at 5.4–6.0‰. The predatory stonefly, *Isogenoides*, possessed the highest invertebrate $\delta^{15}N$ values in this study (range 7.0–8.0‰). Fishes were even more enriched than the invertebrate community (range 8.7–10.5‰), and on average, brook trout had higher $\delta^{15}N$ values than either salmon or dace. Because $\delta^{15}N$ values enrich ≈+3‰ per trophic level (Minagawa and Wada 1984), the trophic position of each fish species (x) could be determined and subsequently used in the isotopic mixing model equation to quantify the relative importance of allochthonous carbon in the diets of fishes at each site.

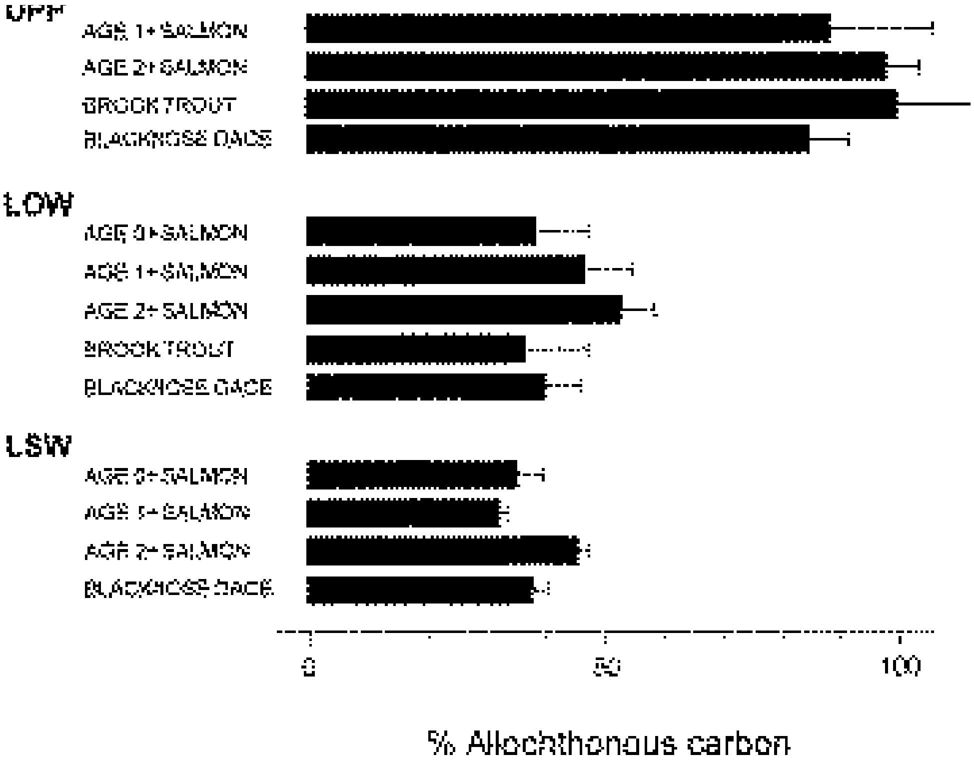
Percent allochthonous carbon

The relative contribution of terrestrial leaf litter inputs (% allochthonous) in the diets of fishes was determined using a two-source isotopic mixing model equation. This model was applied at UPP, LOW, and LSW, where leaf litter and *Cladophora* were shown to be isotopically distinct. Similarity between the $\delta^{13}C$ values of leaf litter and *Cladophora* precluded our attempts to run the model at MID. However, according to the model, fishes at UPP obtained most of their carbon originally from terrestrial sources (Fig. 4). For example, salmon were dependent on terrestrial inputs for 88–98% of their carbon base, while blacknose dace were slightly less dependent at 85%. Brook trout obtained ≈100% of their carbon base from terrestrial sources. At LOW, fishes were less dependent on allochthonous carbon than those in the headwaters, while at LSW fishes derived even less carbon from these inputs (Fig. 4).

Discussion

Our investigations of food webs in Catamaran Brook and the Little Southwest Miramichi River suggest that SIA is a useful tool for measuring the relative contributions of allochthonous and autochthonous carbon in streams. In our study, decomposing leaves were isotopically distinct from algae (*Cladophora*) at all sites except MID. Leaf litter was slightly more depleted than expected for terrestrial C_3 plants, but this likely resulted from the loss of ^{13}C-enriched components during

Fig. 4. Estimates of the relative importance of allochthonous carbon inputs to juvenile Atlantic salmon, brook trout, and blacknose dace at three sites in the Miramichi River system during the 1992–1993 sampling period. Percent allochthonous values were obtained using a two-source isotopic mixing model equation, with terrestrial leaf litter and site-specific *Cladophora* $\delta^{13}C$ values as the two end members. Values are means ± SE.



microbial decomposition (Benner et al. 1987; Rosenfeld and Roff 1992). Differences in *Cladophora* $\delta^{13}C$ among the four sites appeared to reflect a spatial gradient in DIC $\delta^{13}C$, similar to that seen by Kline et al. (1990) and Junger and Planas (1994). The pattern of enrichment in the DIC pool may have resulted from the mixture of ^{13}C-depleted groundwater sources at headwater sites (Oana and Deevey 1960; Rounick and James 1984), with ^{13}C-enriched atmospheric CO_2 (Keeling et al. 1979) along the stream continuum.

Allochthonous carbon appears to be the most important energy source fuelling the benthic fauna in the headwaters of Catamaran Brook. Invertebrates at UPP, with the exception of *Ephemerella*, had $\delta^{13}C$ values that were more similar to those of leaf litter, than to those of either *Cladophora* or *Fontinalis*. Fishes at UPP also had $\delta^{13}C$ values indicative of a greater dependence on leaf litter, and results from the mixing model showed that, on average, >85% of fish carbon was terrestrial in origin. Higher $\delta^{13}C$ values in brook trout may have reflected their larger size (FL $\approx$ 16 cm) and higher trophic position relative to other fishes at this site (Rau et al. 1983).

More extensive sampling at MID is required before we can determine the primary sources of organic carbon driving this food web. Neither leaf litter nor *Cladophora* was depleted enough to account for the low invertebrate $\delta^{13}C$ values measured at this site. Although *Potamogeton* $\delta^{13}C$ was negative enough to account for these values, it was unlikely to be an important energy source because of its relatively low abundance here or at any of the other study sites. The $\delta^{13}C$ of *Glossosoma*, a caddisfly known to graze specifically on diatoms and other fine materials associated with the upper surfaces of rocks (Tindall and Kovalak 1979), suggested assimilation of a more depleted autochthonous carbon source than that represented by *Cladophora*. Unfortunately, biofilm $\delta^{13}C$ was not measured in this study because of previously reported contamination by terrestrially derived detritus (Winterbourn et al. 1984; Rounick and Hicks 1985; Junger and Planas 1994). Although autochthonous carbon appears to be driving the benthic food web at MID, it remains unclear whether or not invertebrate $\delta^{13}C$ values reflect a more ^{13}C-depleted algal carbon source than *Cladophora*, or a detrital link between *Potamogeton* and the benthic food web.

Differences between fish and benthic invertebrate $\delta^{13}C$ values at MID require further investigation as well. Fish were generally too ^{13}C enriched to have derived a significant amount of their carbon base from the sampled invertebrate taxa. It may be that fish were feeding either on invertebrates drifting down from less-depleted upstream areas or on terrestrial insects with distinctly allochthonous carbon labels. Examination of gut contents, however, revealed only small proportions of terrestrial insects in the diets of most fishes at this site (Doucett 1994).

The faunal $\delta^{13}C$ data at LOW and LSW confirm the increasing importance of autochthonous primary production at downstream sites, as would be predicted by the river continuum concept (Vannote et al. 1980). Invertebrate $\delta^{13}C$ values in the lower reach of Catamaran Brook fell between those of leaf litter and *Cladophora*, suggesting a dependence on both resources. Fishes were ^{13}C enriched relative to those located upstream, and exhibited a 39–53% dependence on terrestrial carbon according to the mixing-model equation. High invertebrate δ^{13}C values at LSW suggested that biomass carbon must have been derived mostly from in-situ sources. Autochthonous carbon predominance was also apparent in the fish community at this site, which derived 33–46% of their carbon from terrestrial sources.

δ^{15}N profiles clearly identify food web structure in the headwaters of Catamaran Brook and in the Little Southwest Miramichi River. Despite obvious differences in carbon pathways, nitrogen isotope distributions were almost identical at UPP and LSW, indicating similarity in the δ^{15}N compositions of the primary energy sources and in the patterns of isotopic fractionation within each food chain. Fishes had δ^{15}N values that were ≈8–10‰ above the primary food sources, suggesting 2.5–3.5 trophic levels in these streams. These findings were consistent with estimates of stream trophic structure from other studies using δ^{15}N values (Estep and Vigg 1985; Fry 1991).

Seasonal changes in the δ^{13}C of age 0+ salmon emphasize the value of SIA for investigating temporal changes in the energetic pathways of fish communities. Maternally derived marine carbon was likely responsible for higher δ^{13}C values in postemergent age 0+ salmon. Because Atlantic salmon migrate to the open ocean to grow and mature, adults returning to spawn in Catamaran Brook possess δ^{13}C values (≈–18‰; Doucett 1994) that reflect marine primary production (≈–21‰; Peterson and Fry 1987). Subsequent dilution of stored marine carbon in the tissues of recently emerged age 0+ salmon following feeding in freshwater likely resulted in more ^{13}C-depleted values later in the growing season.

In contrast, lack of seasonality in the δ^{13}C values of age 1+ and age 2+ salmon suggest that isotope ratios in older parr reflect longer term diet. Turnover in animal δ^{13}C is related to growth rate (Fry and Arnold 1982; Tieszen et al. 1983), and older fish take longer to reflect changes in dietary δ^{13}C than smaller fish (Hesslein et al. 1993). Therefore, unlike the carbon pool of age 0+ salmon, which is either turned over or diluted during the summer months, the δ^{13}C values of older parr represent food sources assimilated over two or more seasons. Obtaining estimates of carbon turnover times for different age-classes of Atlantic salmon parr will be a crucial step in understanding potential changes in fish δ^{13}C values that may follow deforestation in the Catamaran Brook basin.

SIA appears to have great potential as an effective fisheries management tool because it provides a means by which the energy basis for secondary production can be determined. In this study, the relative importance of allochthonous carbon in stream food webs leading to wild juvenile Atlantic salmon was quantified using a combination of stable carbon and nitrogen isotope ratios. Estimates from an isotopic mixing model equation showed that fishes obtained most of their carbon from allochthonous sources in the headwaters, but in downstream sites, autochthonous inputs played an equally important role. These results are consistent with the river continuum concept (Vannote et al. 1980). Small forested streams, such as Catamaran Brook, are closely linked to their surrounding catchments, and inputs from the terrestrial environment are regarded as principal energy sources fuelling benthic communities in headwater sites (Hynes 1975). Moving downstream into the Little Southwest Miramichi River, open canopies allow increased solar radiation to stimulate higher autochthonous production. A similar study on a small New Zealand catchment (Rounick et al. 1982; Rounick and Winterbourn 1986) showed that SIA has the potential to resolve changes in the nature of the food base following forest removal. In this study, *Deleatidium*, a browsing mayfly, came to depend more on autochthonous carbon sources over a 9-year period after cutting. As the Catamaran Brook basin is scheduled for logging in 1996–1999 (Cunjak et al. 1990), continued sampling efforts should show the value of the SIA technique for investigating trophic responses of fish communities to environmental change.

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