STABLE-CARBON-ISOTOPE RATIOS OF RIVER BIOTA: IMPLICATIONS FOR ENERGY FLOW IN LOTIC FOOD WEBS

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Abstract. Stable-isotope ratios of carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) have been widely used to determine the energy base of stream food webs, but such use is controversial due to unexplained variability in algal $\delta^{13}C$. I used published $\delta^{13}C$ data from temperate headwater streams through medium-sized rivers (0.2–4000 km^2 watershed area) collected during summer baseflows and original data from streams in northern California to analyze energy pathways through river food webs. The analyses showed three important results. First, epilithic algal $\delta^{13}C$ and watershed area are positively related, suggesting that effects of carbon limitation on algal carbon uptake result in ^{13}C enrichment of algal $\delta^{13}C$ in larger, more productive rivers. Second, epilithic algae and terrestrial detritus $\delta^{13}C$ values are often distinct in small shaded streams but overlap in some larger unshaded streams and rivers. Measurements of $\delta^{13}C$ values may be most useful in distinguishing algal and terrestrial energy sources in unproductive streams with supersaturated dissolved CO_2 concentrations, and some productive rivers where CO_2 concentrations are low relative to photosynthetic rates. Finally, consumer $\delta^{13}C$ values are more strongly related to algal $\delta^{13}C$ than terrestrial $\delta^{13}C$. The relative contribution of terrestrial and algal carbon sources often varied by functional feeding group within and between sites. However, with the exception of shredders and scrapers, which respectively relied on terrestrial and algal carbon sources, patterns of consumer $\delta^{13}C$ clearly show a transition from terrestrial to algal carbon sources for many lotic food webs in streams with ≥ 10 km^2 watershed area. The observed transition to algal carbon sources is likely related to increasing primary production rates as forest canopy cover declines in larger streams, although decreasing retention or quality of terrestrial carbon may also play a role. Improved analyses of algal $\delta^{13}C$ and $\delta^{15}N$ combined with quantitative study of organic matter dynamics and food web structure should allow the relative importance of these factors to be distinguished in future food web studies.

Key words: algae; carbon limitation; $\delta^{13}C$; energy flow; lotic food webs; stable-carbon-isotope ratios; terrestrial detritus; watershed area.

INTRODUCTION

Identifying the trophic base of food webs is fundamental to understanding the dynamics of populations, communities, or ecosystems. Identifying the sources of production for lotic food webs remains a major challenge to stream ecologists, because of the complexity of controls over carbon sources, the small size of stream organisms, and the mobility of top predators (Allan 1995). The standing stocks and fluxes of organic carbon in river ecosystems are relatively well described (Vannote et al. 1980, Webster and Meyer 1997). These observations influenced a descriptive model of stream ecosystem structure and function (i.e., the River Continuum Concept) that suggests a transition from terrestrial carbon sources for food webs in headwater streams to algal and terrestrial sources for food webs in mid-order reaches of rivers (Vannote et al. 1980). While this model is the main framework for under-

standing energy flow in streams and small rivers, the processes that control the transfer of potential organic matter sources through local stream or river food webs remain poorly understood (e.g., Wallace et al. 1997).

Measurements of stable-carbon-isotope ratios ($^{13}C/^{12}C$ or $\delta^{13}C$) hold much promise as a tool for understanding energy flow in river food webs for three reasons. First, $\delta^{13}C$ values are effective diet tracers in food webs because there is little isotopic fractionation with trophic transfer of organic carbon (DeNiro and Epstein 1978, France 1996a). Second, primary production in adjacent habitats or ecosystems often has different $\delta^{13}C$ values due to variation in plant physiology, inorganic carbon sources, or resource availability (Rounick and Winterbourn 1986, Peterson et al. 1993, Bunn et al. 1997, Finlay et al. 1999). Finally, consumer $\delta^{13}C$ integrate prey $\delta^{13}C$ over relatively long periods of time (weeks to years depending on body size and growth rate), offering distinct advantages over techniques such as gut-content analysis.

Stable-carbon-isotope analyses have been widely used to assess the contribution of terrestrial detritus and algal production to river food webs, because terrestrial and aquatic plants often have different $\delta^{13}C$

values (Rounick and Winterbourn 1986). Stable-carbon-isotope analyses of river food webs have been essential to demonstrating the importance of algal production to consumers in ecosystems that appeared to be strongly heterotrophic due to the abundance of detritus or low ratio of primary production to heterotrophic metabolism (Hamilton et al. 1992, Peterson et al. 1993, France 1995). Nonetheless, controversy over the application of stable-carbon-isotope analyses in streams has arisen due to unexplained variability in algal and consumer $\delta^{13}C$ within and between sites, and the lack of true epilithic algal endpoints for stable-carbon-isotope mixing models (France 1995, 1996*b*, Doucett et al. 1996*a*, Finlay et al. 1999). While stable-carbon-isotope ratios of C3 terrestrial plant detritus in streams are relatively constant at about $-28‰$ (France 1995), freshwater lotic algal $\delta^{13}C$ range between -47 and $-12‰$ (France 1995, Finlay et al. 1999).

As in many other aquatic environments, stable-carbon-isotope-ratios of benthic algae in lotic ecosystems are determined by the $\delta^{13}C$ of dissolved inorganic carbon (DIC), and the amount of fractionation, or discrimination against ^{13}C, during carbon uptake and assimilation (Keeley and Sandquist 1992). The relative contribution of three DIC sources (weathering, atmosphere, and respiration) determines streamwater $\delta^{13}C$ DIC (Hitchon and Krouse 1972, Mook and Tan 1991). The amount of fractionation during photosynthesis is generally determined by supply (i.e., concentration and water velocity) relative to demand (i.e., algal photosynthetic rates) for CO_2, the most available form of inorganic carbon to aquatic plants. In river food web studies that have used stable carbon isotope methods, $\delta^{13}C$ DIC are often measured, while effects of supply and demand for carbon, hereafter ''carbon limitation,'' on algal $\delta^{13}C$ are rarely assessed (see Finlay et al. 1999).

Much of the difficulty in assessing the controls of algal $\delta^{13}C$ in streams stems from the inability to measure epilithic algal $\delta^{13}C$ directly. Measurements of algal $\delta^{13}C$ are problematic due to the low standing crop of algae relative to detritus and heterotrophs in epilithic films, especially in shaded headwater streams. Attempts to use $\delta^{13}C$ of other autotrophs, such as mosses or filamentous algae, to infer epilithic algal $\delta^{13}C$ are problematic due to differences in physiology and growth form between these plants and epilithic algae (Raven et al. 1982, Steinman et al. 1992). In the analyses presented here, I compiled published food web carbon isotope data and used $\delta^{13}C$ of known invertebrate consumers of epilithic algae to infer algal $\delta^{13}C$ when direct measurements of epilithic algal $\delta^{13}C$ were not available. When possible, I checked the assumption that herbivore $\delta^{13}C$ represented algal $\delta^{13}C$, and found a good agreement between the two variables. I used these estimates of algal $\delta^{13}C$ to assess the relative importance of $\delta^{13}C$ DIC and effects of carbon limitation in controlling epilithic algal $\delta^{13}C$ along a gradient in

watershed area. Using site-specific estimates of algal and terrestrial detritus $\delta^{13}C$, I then analyzed the role of algal and terrestrial carbon sources in explaining consumer $\delta^{13}C$ in lotic food webs.

METHODS

General approach and data organization

To explore the controls of algal $\delta^{13}C$ and patterns of energy flow in lotic ecosystems, I compiled published stable-carbon-isotope data from studies of temperate and Arctic streams and rivers. Physical and chemical parameters, and $\delta^{13}C$ data for DIC, detritus, algae, invertebrates and fish collected under summer baseflow conditions were compiled from 70 sites and 26 published studies. Only data collected during summer were used to minimize effects of temporal variability, to allow intersite comparisons, and because sampling in most studies was limited to a single summer date or month. Data were not included in the analyses if they were not site specific (i.e., if data were averaged over several distinct sites for a species or group), or if they were collected in experimentally treated or excessively disturbed watersheds (i.e., logged, burned, fertilized, or otherwise manipulated), sites immediately downstream of dams or lakes, or sites that had large runs of semelparous anadromous salmon. Data from watersheds with predominantly C4 or CAM vegetation were also excluded. Data used were not corrected for lipid concentrations (e.g., McConnaughey and McRoy 1979) or trophic position (e.g., Kline et al. 1998). Post hoc corrections for trophic position were not made because there is no consensus concerning the amount of trophic fractionation of $\delta^{13}C$ for freshwater consumers (France 1996*a*).

In some cases, data not included in an original manuscript were provided by the original author, by related references, or, for watershed areas in several cases, from topographic maps. Watershed areas not included in the original manuscript but provided here are approximate when the exact sampling location could not be determined. Previously unpublished $\delta^{13}C$ data for DIC and consumers in streams and rivers in Northern California are reported here. Methods associated with sample collection and analyses are detailed below and in Finlay et al. (1999).

Stable-carbon-isotope data for riparian vegetation consisted of values for live leaves of common riparian plants. Coarse particulate organic matter (CPOM) most frequently represented samples of conditioned terrestrial leaf litter collected from the streambed, but also included samples of unsorted coarse detritus in a few cases. Fine particulate organic matter (FPOM) was benthic organic matter sorted to include particles 0.5 μm–1 mm in diameter. Dissolved organic carbon (DOC) consisted of dissolved organic matter < 0.5μm. Transported particulate organic matter or seston $\delta^{13}C$ were

reported for a small subset of sites, and were not considered further in the analyses.

Stable-carbon-isotope data for algae were separated into epilithic and filamentous groups. Data were used for epilithic algae only if the material sampled was predominantly algal as determined by observation or chlorophyll analysis; data from general scrapings of epilithic material, which are most often reported, were not included. Invertebrates were grouped into functional feeding groups (i.e., scrapers, shredders, filterers, collector-gatherers, predators) based on authors' designations or Merritt and Cummins (1996). Stable-carbon-isotope ratios of individual species or genera were averaged by functional feeding group at each site.

I restricted analyses of an additional category, herbivores, to those invertebrate grazers that consumed significant amounts of epilithic algae. All scrapers were designated herbivores; collector-gatherers (hereafter ''collectors'') were also considered herbivores if they fed on epilithic films, and if gut content analysis indicated that a significant diet fraction was composed of algae or if collector $\delta^{13}C$ were distinct (by at least 3‰) from terrestrial detritus or shredder $\delta^{13}C$. Collectors that fed on or in filamentous algae were not included as herbivores. Herbivores, as defined above, were identified at most sites that reported invertebrate $\delta^{13}C$.

I focused on analyses of epilithic algae for three reasons. First, this is the most common and important general algal growth form in small to midsized streams and rivers (Allan 1995). Second, the growth form of epilithic algal films should be the least variable among sites. Examination of large-scale patterns in algal $\delta^{13}C$ requires holding growth form constant because algal morphology affects acquisition of inorganic carbon and nutrients in stream algae (Steinman et al. 1992). Finally, the cell density and patch size of filamentous or colonial algae collected for $\delta^{13}C$ analysis are seldom reported. These factors may vary widely and strongly influence algal $\delta^{13}C$ (Calder and Parker 1973, Pardue et al. 1976).

At sites where investigators separated algae in epilithic films from other material for $\delta^{13}C$ measurement, the algal $\delta^{13}C$ were used in subsequent watershed area and food web analyses. At all other sites, herbivore $\delta^{13}C$ were used to infer epilithic algal $\delta^{13}C$. I used herbivores to infer algal $\delta^{13}C$ because it is extremely difficult to isolate pure samples of the epilithic microalgae that constitute the base of many freshwater food webs from other organic matter or heterotrophs, and consequently few data for epilithic algae $\delta^{13}C$ exist. This approach may have introduced four forms of additional complexity into analyses of algal $\delta^{13}C$. First, trophic transfer of organic carbon is associated with increases in consumer $\delta^{13}C$ of up to 1‰ (DeNiro and Epstein 1978), although France (1996a) suggests that enrichment factors may be somewhat lower for freshwater consumers.

The second possible complexity introduced by using herbivore $\delta^{13}C$ to infer algal $\delta^{13}C$ is the potential consumption by herbivores of terrestrially derived carbon with a different $\delta^{13}C$ from that of algae. Assimilation of terrestrial detritus would also complicate food web analyses, since algal and detrital $\delta^{13}C$ may overlap. Invertebrates classed as herbivores may have consumed and assimilated terrestrial detritus or heterotrophic organisms that relied on terrestrial detritus, particularly in forested headwater streams where algal productivity is low relative to detritus availability. However, the high food quality and turnover rates of algae may make algal production more important to herbivore diets than suggested by its low abundance relative to detritus (e.g., Mayer and Likens 1987, Hamilton et al. 1992, Peterson et al. 1993).

Third, one criterion used to classify herbivores (i.e., collector $\delta^{13}C$ distinct from terrestrial carbon $\delta^{13}C$ by 3‰) may have biased the estimates of algal $\delta^{13}C$ against overlap with terrestrial carbon $\delta^{13}C$ in headwater streams, particularly if algal $\delta^{13}C$ were variable within a site. However, investigation of controls of algal $\delta^{13}C$ in lotic ecosystems suggests that variability in algal $\delta^{13}C$ is small where algal production is low and dissolved CO_2 (i.e., $CO_{2(aq)}$) availability is high (MacLeod and Barton 1998, Finlay et al. 1999), as often observed in headwater streams.

Finally, selective grazing or assimilation of algal species by herbivores could bias estimates of algal $\delta^{13}C$ if there are differences in carbon acquisition among the algal taxa that compose epilithic films. Despite these potential limitations, I believe the use of herbivore $\delta^{13}C$ to infer algal $\delta^{13}C$ makes the best use of published data for developing hypotheses to explain controls of algal $\delta^{13}C$ and assessing the role of algal production in lotic food webs.

Fish $\delta^{13}C$ were averaged for species that were predominately aquatic invertebrate feeders, although many taxa likely fed partially on terrestrial invertebrates or other fish. Fish data from species that relied primarily on terrestrial invertebrates were excluded.

Original data for Northern California streams

Original $\delta^{13}C$ data for DIC and consumers at sites described in Finlay et al. (1999) are reported here. Sites ranged from heavily shaded primary streams to unshaded, productive reaches of the South Fork Eel River in the Coast Range of Northern California. Samples for $\delta^{13}C$ DIC were collected in mid-July 1997 from well-mixed streamwater during early afternoon. Bubble-free samples were collected in glass bottles and sealed with Teflon septa after preservation with saturated $HgCl_2$. Samples were refrigerated in the dark until analyses. Samples were acidified with 100% phosphoric acid, and the resulting CO_2 was collected and purified cryogenically. The purified CO_2 was analyzed on a Micromass Prism mass spectrometer. The standard deviation for

sample analysis was usually <0.01‰, and the standard deviation of duplicate samples was 0.33‰.

Similarly, original consumer δ^{13}C data, and data modified from Finlay et al. (1999), for epilithic algae, invertebrate functional feeding groups, and fish (juvenile steelhead trout, and roach, in the two largest sites) were collected in mid-July 1997. For fish δ^{13}C in the three largest sites (Elder Creek, South Fork Eel River, and Ten Mile Creek) only data for fish collected from pools were included, since these habitats are the largest in areal extent. Sample collection procedures, taxa, and analytical methods are described in Finlay et al. (1999).

Watershed area relationships

Data for factors that might determine algal δ^{13}C other than δ^{13}C DIC (i.e., $CO_{2(aq)}$ supply, and photosynthetic rates) are rarely reported in stable-carbon-isotope investigations of lotic food webs. As a consequence, all the information necessary to identify the controls of algal δ^{13}C is not available. For this reason, I used watershed drainage area as a proxy for carbon supply ($CO_{2(aq)}$) relative to demand (photosynthetic rates) in small to midsized rivers. This approach is justified because across the range of watershed areas examined here, $CO_{2(aq)}$ decreases with distance downstream (e.g., Lorah and Herman 1988, Dawson et al. 1995, Jones and Mulholland 1998, Finlay et al. 1999), while photosynthesis rates (or gross primary production) increase due to decreased canopy cover, and greater light penetration and warmer temperatures (Lamberti and Steinman 1997). Thus, $CO_{2(aq)}$ supply should be large relative to demand in small watersheds, and low relative to demand in larger watersheds. If effects of carbon limitation are important in determining algal δ^{13}C in more productive rivers, then algal δ^{13}C should increase as a function of watershed area. If algal production is important to consumer diets, then consumer δ^{13}C should track changes in algal δ^{13}C with watershed area. Linear regression was used to analyze the relationship of δ^{13}C DIC and food web components with log-transformed values of watershed area. Slopes for regression models were analyzed with t tests ($P < 0.05$).

Food web relationships

To test for enrichment in ^{13}C during decomposition of terrestrial detritus, I used Wilcoxon signed-rank tests on paired data for riparian vegetation and conditioned leaves from the same taxa at the same site, and one-way ANOVA to compare δ^{13}C values of riparian vegetation, CPOM, FPOM, and DOC. Means were compared using Tukey HSD ($P < 0.05$).

I used multiple regressions to determine the role of terrestrial and algal carbon sources in stream food webs. Terrestrial detritus δ^{13}C were estimated from site-specific CPOM δ^{13}C in most cases because CPOM should be the most representative and best-integrated measurement of terrestrial δ^{13}C available. In several shaded headwater streams where CPOM data were not available, FPOM δ^{13}C were used for terrestrial detritus δ^{13}C since it is unlikely that algal carbon enters the FPOM pool in unproductive streams, and since there were no significant differences between CPOM and FPOM. In two studies, CPOM δ^{13}C were measured at one site in a watershed where several sites were investigated. In these cases, average CPOM δ^{13}C from the single site were used to represent terrestrial detritus δ^{13}C at other sites in the watershed, since there were no trends in CPOM δ^{13}C with watershed area. Epilithic algal δ^{13}C were represented by algal (A) δ^{13}C, or herbivore (H) δ^{13}C, as defined for this study, where algal data were not available. When algal and herbivore δ^{13}C were used to infer algal δ^{13}C in food web analyses, algal carbon sources are referred to as AH δ^{13}C. Slopes of regression models were evaluated statistically as for watershed area relationships.

RESULTS

Study sites were predominantly located in temperate forested watersheds of North America and New Zealand. The watershed areas of these sites ranged from 0.2 to 4050 km^2 (Table 1).

Watershed area relationships

Stable-carbon-isotope ratios of riparian vegetation, terrestrial detritus (CPOM and FPOM), and DOC showed no trends with watershed area (Fig. 1). Stable-carbon-isotope ratios of DIC showed a weak positive trend with watershed area (Fig. 2). δ^{13}C DIC of cold spring streams sampled at or near the source were not included in the analysis because the watershed areas were unknown. Average δ^{13}C DIC of -18.9 ± 1.3‰ (mean $\pm$ 1 SE) at these sites (62–64, Table 1) were strongly depleted relative to river water, consistent with the supersaturation of respiratory CO_2 often found in spring environments (Rounick and James 1984).

In contrast, algal and herbivore δ^{13}C were strongly correlated with watershed area (Fig. 2). Since herbivore δ^{13}C, used to infer algal δ^{13}C in most cases, could have been affected by consumption of terrestrial carbon in shaded headwater streams and larger rivers, the positive relationship between algal δ^{13}C and watershed may be conservative. However, where epilithic algal δ^{13}C were measured, herbivore δ^{13}C closely matched values for algae (Fig. 3). The relationship between these groups was highly significant and showed no consistent increase or decrease in herbivore δ^{13}C relative to algal δ^{13}C.

Algal and herbivore δ^{13}C in headwater streams were distinct from values in larger rivers by at least 4‰ (Fig. 2). Streams and rivers with high algal δ^{13}C were characterized by relatively open canopies or high levels of algal biomass. Data from studies not included in these analyses because watershed areas could not be determined (e.g., Lester et al. 1995) were consistent with this pattern. Algal and herbivore δ^{13}C were most de-

TABLE 1. Location and site characteristics for studies used in analyses of stable-carbon-isotope data.

Study	Site	ID	Type	Watershed area (km²)	Canopy cover (%)
Schiff et al. (1997)	Harp 3a	1	F	0.2	...
Rounick et al. (1982)	Middle Bush Stream	2	F	0.3	80
Hall (1995)	Cold Spring	3	F	0.4	99
Kendall et al. (1992)	Shelter Run	4	F	0.5	...
Winterbourn et al. (1984)	Devils Creek, Site 1	5	F	0.5	...
Finlay et al. (1999; *unpublished data*)	McKinley Creek	6	F	1.0	98
Schiff et al. (1997)	Harp 4	7	F	1.4	...
Finlay et al. (1999; *unpublished data*)	Skunk Creek	8	F	1.4	97
Schiff et al. (1997)	Harp 5	9	F	2.1	...
Rosenfeld and Roff (1992)	Limestone Creek	10	F	2.2	85
Kendall et al. (1992)	Owens Creek	11	F	2.6	...
Bilby et al. (1996)	Stream 0372	12	F	2.7	99
Finlay et al. (1999; *unpublished data*)	Fox Creek	13	F	3.0	98
Winterbourn et al. (1984)	Devils Creek, Site 2	14	F	3.0	...
McArthur and Moorhead (1996)	Meyers Branch, Upper	15	F	5.6	...
Junger and Planas (1994)	De l'Aqueduc Creek	16	F	6.0	30
Rosenfeld and Roff (1992)	App's Mill Creek	17	F	6.5	85
Winterbourn et al. (1984)	Devils Creek, Site 3	18	F	7.0	...
Winterbourn et al. (1984)	Devils Creek, Site 4	19	F	8.0	...
Winterbourn et al. (1984)	Devils Creek, Site 5	20	F	10.0	...
Doucett et al. (1996b)	Catamaran Brook - UPP	21	F	12.0	...
Keough et al. (1998)	Bear Creek	22	F	12.3	...
Rosenfeld and Roff (1992)	Carrol Creek	23	F	13.1	85
Keough et al. (1998)	Bluff Creek	24	F	16.7	...
Rounick et al. (1982)	Grasmere Stream	25	TG	17.0	5
Finlay et al. (1999; *unpublished data*)	Elder Creek, riffle	26	F	17.0	86
Finlay et al. (1999; *unpublished data*)	Elder Creek, pool	27	F	17.0	86
Bilby et al. (1996)	Ten Creek	28	F	18.0	99
Kline et al. (1990)	Sashin Creek, Site 3	29	F	18.0	...
Rounick and Hicks (1985)	Mangaone Stream	30	F	19.0	10
Peterson et al. (1994)	Essex River	31	F	23.0	...
Doucett et al. (1996b)	Catamaran Brook, MID	32	F	25.0	...
Rounick and Hicks (1985)	Horokiri Stream Back Branch	33	F	25.0	0
Rounick and Hicks (1985)	Horokiri Stream Road Branch	34	F	30.0	50
Rosenfeld and Roff (1992)	Swan Creek	35	F	30.6	0
McArthur and Moorhead (1996)	Meyers Branch, Middle	36	F	34.2	...
Simenstad and Wissmar (1985)	Big Beef Creek	37	F	38.0	...
Garman and Macko (1998)	Wards Creek	38	F	42.7	...
Doucett et al. (1996b)	Catamaran Brook, LOW	39	F	52.0	...
Fry (1991)	Lower Lookout Creek	40	F	60.5	...
McArthur and Moorhead (1996)	Meyers Branch, Lower	41	F	78.4	...
Rounick and Hicks (1985)	Waikanae River	42	F	118	80
Finlay et al. (1999; *unpublished data*)	Eel River, riffle	43	F	130	39
Finlay et al. (1999; *unpublished data*)	Eel River, riffle	44	F	130	39
Peterson et al. (1993)	Kuparuk River	45	T	150	5
Angradi (1993)	Buffalo River	46	F	153	...
Peterson et al. (1994)	Ipswich River	47	F	155	...
Simenstad and Wissmar (1985)	Duckabush River	48	F	172	...
Finlay et al. (1999; *unpublished data*)	Ten Mile Creek, riffle	49	F	180	7
Finlay et al. (1999; *unpublished data*)	Ten Mile Creek, pool	50	F	180	7
Winterbourn et al. (1984)	Inangahua River	51	F	200	...
Collier and Lyon (1991)	Manganuiateao River, M6	52	F	261	5
Junger and Planas (1994)	Montmorency River	53	F	265	0
Collier and Lyon (1991)	Manganuiateao River, M8	54	F	322	5
Simenstad and Wissmar (1985)	Skokomish River	55	F	366	...
Whitledge and Rabeni (1997)	Jacks Fork River	56	F	384	0
Peterson et al. (1994)	Parker River	57	F	404	...
Doucett et al. (1996b)	Little Southwest Miramichi River	58	F	1200	...
Angradi (1993)	Henrys Fork River	59	F	1264	...
Bunn et al. (1989)	Korac River, Mainstem	60	T	4050	0

TABLE 1.   Continued.

Study	Site	ID	Type	Watershed area (km²)	Canopy cover (%)
Keough et al. (1998)	Unnamed tributary stream	61	F	⋯	⋯
Osmond et al. (1981)	Ryovarinkuoppa	62	CS	⋯	⋯
Osmond et al. (1981)	Runebergin	63	CS	⋯	⋯
Rounick and James (1984)	Cold springs	64	CS	⋯	⋯
Rounick and James (1984)	Orakeikorako	65	WS	⋯	⋯
Rounick and James (1984)	Waipahih	66	WS	⋯	⋯
McDowell et al. (1996)	Black Creek	67	F	⋯	⋯
M.J. Winterbourn and J.S. Rounick (*unpublished data*; cited in Rounick et al. [1982])	Maimai stream	68	TG	⋯	⋯
Junger and Planas (1993, 1994)	Laflamme Creek	69	F	⋯	90
Schiff et al. (1997)	Harp 4–21	70	F	⋯	⋯

Notes: "Type" indicates dominant watershed vegetation or spring type: F = forested, TG = tussock grassland, T = tundra, CS = cold spring, WS = warm spring.

pleted in cold-water springs, and poorly drained, low-gradient streams with areas of wetlands within the watershed (e.g., Sites 25, 35, 63 in Table 1), indicating the importance of respiratory $CO_{2(aq)}$ as an inorganic carbon source for algae in these ecosystems. Algal and herbivore δ¹³C were largely distinct from terrestrial detritus δ¹³C in headwater streams, overlapping most often in open-canopied rivers (Fig. 2).

Patterns in scraper δ¹³C (Fig. 4a) were similar to those observed for algae (Fig. 2). In contrast, shredder δ¹³C showed no trend with watershed area (Fig. 4b) and were often similar to CPOM δ¹³C (Fig. 1), consistent with primary reliance on terrestrial carbon sources. However, ¹³C-depleted or -enriched shredder δ¹³C relative to local terrestrial carbon sources at sites characterized by open canopies or high levels of algal pro-duction (e.g., Sites 35, 50 in Table 1) suggest the role of algal carbon to shredders at some sites.

The relationships of collector, filter feeder, and invertebrate predator δ¹³C with watershed area were more complex, but the pattern observed for algal δ¹³C was also evident for these functional feeding groups (Fig. 4c–e). In the smallest headwater streams, δ¹³C values for the three groups closely matched terrestrial detritus δ¹³C, but downstream ¹³C depletion (e.g., Sites 10, 17, 20), and enrichment farther downstream in larger streams and rivers demonstrated increased reliance on algal carbon as stream size increased and canopy cover decreased.
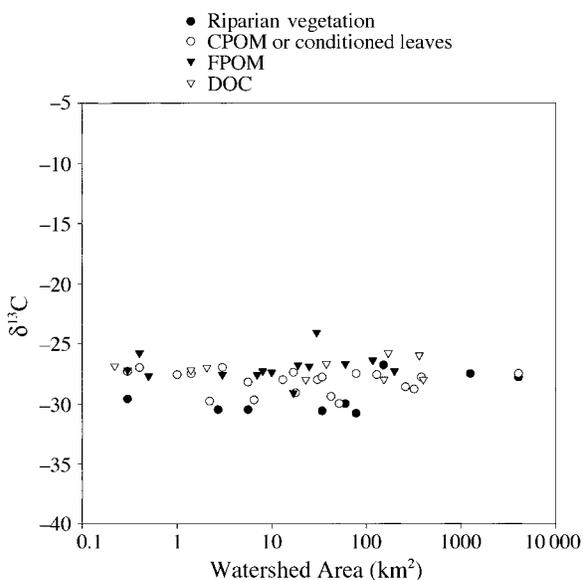
The relationship between fish δ¹³C and watershed

FIG. 1.   Relationship of live foliage from riparian vegetation, CPOM, FPOM, and DOC δ¹³C and watershed area. Regression slopes were nonsignificant with r^2 around zero in each case except for riparian vegetation ($P = 0.08$, $r^2 = 0.29$).
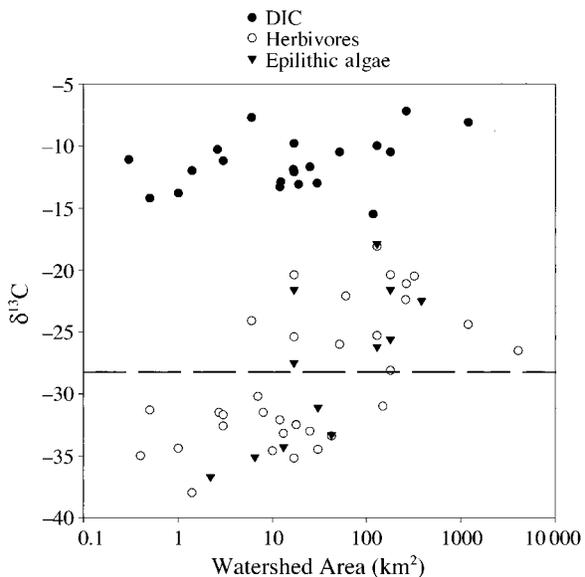

FIG. 2.   Relationship of DIC, epilithic algae, and herbivore δ¹³C and watershed area. The regression slope was nonsignificant ($P = 0.1$, $r^2 = 0.09$) for DIC δ¹³C, but significant for combined algae and herbivore δ¹³C ($P < 0.001$, $r^2 = 0.46$). For reference, dashed lines represent δ¹³C ($-28.2 \pm 0.2‰$ [mean $\pm$ 1 SE]) for CPOM for all sites in Table 1.
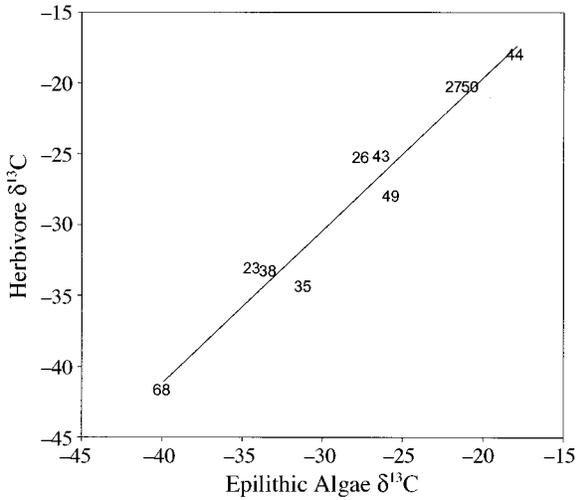
FIG. 3. Relationship of epilithic algal $\delta^{13}C$ and herbivore $\delta^{13}C$. The slope for a linear regression model was highly significant ($y = 2.34 + 1.1x$, $P < 0.001$, $r^2 = 0.94$).

area were more clear because fish were absent from the smallest headwaters streams. Fish $\delta^{13}C$ were positively related to watershed area (Fig. 4f); fish $\delta^{13}C$, which should increase by 1–2‰ relative to the carbon source of their prey depending on trophic level (DeNiro and Epstein 1978), were depleted in some headwater streams relative to terrestrial detritus, suggesting the importance of algal carbon to top predators in relatively unproductive streams.

Food web relationships

Terrestrial carbon sources showed small but consistent ^{13}C-enrichment during decomposition. For paired data ($n = 3$), live foliage from riparian vegetation (-28.9 ± 1.0‰) was marginally significantly depleted ($P = 0.054$) relative to stream-conditioned leaves (-27.2 ± 0.6‰) (data from Sites 2 and 69 in Table 1, and Mihuc and Toetz 1994, *Salix* only). Means of all values for each category showed a similar pattern. Riparian vegetation (-29.3 ± 0.5‰, $n = 9$) was significantly ^{13}C-depleted relative to CPOM (-28.2 ± 0.2‰, $n = 22$), and CPOM was significantly depleted relative to FPOM (-27.0 ± 0.3‰, $n = 14$). DOC (-27.1 ± 0.3‰, $n = 10$) was not significantly enriched relative to CPOM or FPOM.
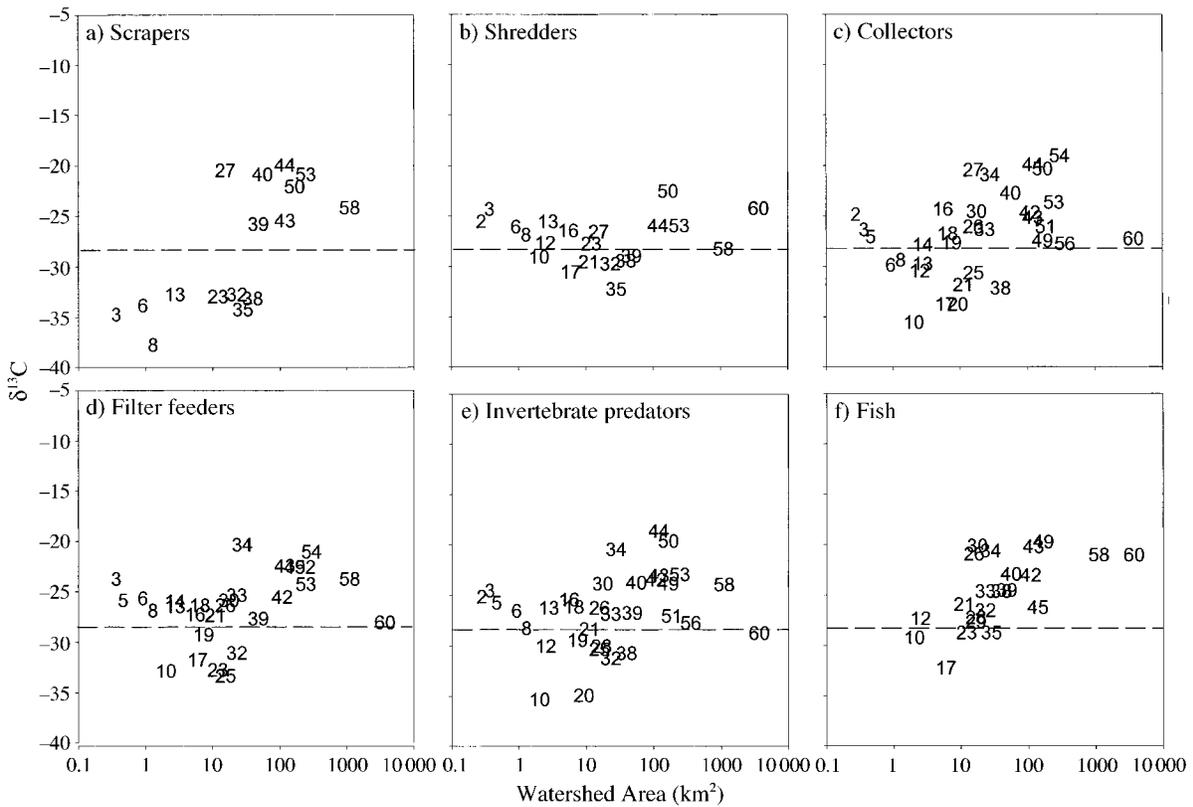

FIG. 4. Relationship of (a) scraper, (b) shredder, (c) collector, (d) filter feeder, (e) invertebrate predator, and (f) fish $\delta^{13}C$ and watershed area. The slope for a linear regression model was significant for scrapers ($P = 0.002$, $r^2 = 0.48$), collectors ($P = 0.03$, $r^2 = 0.12$), and fish ($P = 0.001$, $r^2 = 0.34$). For reference, dashed lines represent $\delta^{13}C$ (-28.2 ± 0.2‰ [mean ± 1 SE]) for CPOM for all sites in Table 1.
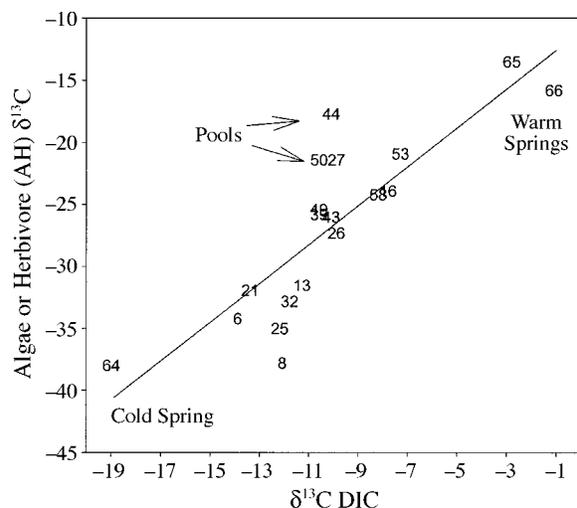
FIG. 5. Relationship of AH δ^{13}C and δ^{13}C dissolved inorganic carbon (DIC). The slope for a linear regression model was highly significant ($y = -11.0 + 1.6x$, $P < 0.001$, $r^2 = 0.68$).

Algal δ^{13}C inferred from direct measurements and herbivore δ^{13}C (i.e., AH δ^{13}C) were strongly related to δ^{13}C DIC (Fig. 5), although very little data from larger rivers were available. Values for pool algae δ^{13}C were high relative to the relationship derived from the regression analyses (Fig. 5). Water velocity, shown to affect algal δ^{13}C in productive rivers with low levels of $CO_{2(aq)}$ (Finlay et al. 1999), was rarely reported, so that the overall effect of this variable could not be assessed.

Multiple regressions showed that algal carbon sources were more significant in explaining consumer δ^{13}C than terrestrial detritus for most groups. Relationships between AH δ^{13}C and consumer δ^{13}C were highly significant for all groups except shredders (Table 2). AH δ^{13}C explained the least variation in invertebrate δ^{13}C in small (i.e., <10 km² watershed area) streams (Fig.

4b–e). In contrast, relationships between terrestrial detritus and consumer δ^{13}C were not significant for scrapers, invertebrate predators, and fish.

For complete reliance on either algae or terrestrial detritus, the coefficients of significant relationships between consumer and organic matter source δ^{13}C should be ~1. For some relationships this was not the case (Table 2). Algal carbon sources were clearly not important to most functional feeding groups in the smallest headwater streams (Fig. 4), and this lack of fit to regression models altered algal–consumer coefficients. Removing streams smaller than 10 km² watershed area from the multiple regression analyses increased the slopes of relationships between algal and filter feeder, collector, and invertebrate predator δ^{13}C to around 0.65–0.7, and did not affect algal–shredder relationships (data not shown). In contrast, no relationships between terrestrial detritus and consumer δ^{13}C were significant with data for headwater steams removed except for shredders. Other factors, such as temporal variation in epilithic algal or terrestrial detritus δ^{13}C, or consumption of filamentous algae by consumers, may account for the remaining unexplained variation in consumer δ^{13}C.

The multiple regression analyses made three important assumptions that were largely supported by the data. The first assumption was that CPOM and conditioned leaf δ^{13}C represented available terrestrial carbon δ^{13}C. Between-site differences in CPOM δ^{13}C were small, suggesting limited spatial variation in stable-carbon ratios of terrestrial inputs to streams. Further, differences between CPOM and other terrestrially influenced detrital fractions (i.e., FPOM and DOC) were small. Together, these results indicate that CPOM δ^{13}C adequately represented terrestrial carbon δ^{13}C.

The second assumption was that herbivore δ^{13}C represented algal δ^{13}C. The strong relationship between these groups (Fig. 3) in open canopied sites suggests that this assumption was valid in more productive

TABLE 2. Multiple regression results from analyses of carbon sources (terrestrial detritus and algae) and stream consumer δ^{13}C.

| Consumer | Whole-model r^2 | Terrestrial detritus δ^{13}C | | | AH δ^{13}C | | |
		Coefficient	P	r_{TD}	Coefficient	P	r_{AH}
Scraper	0.87	0.50 ± 1.70	0.785	0.00	0.90 ± 0.18	0.007	0.89
Shredder	0.48†	1.26 ± 0.34	0.002	0.67	0.08 ± 0.07	0.235	0.13
Collector	0.81	2.07 ± 0.63	0.007	0.26	0.50 ± 0.09	<0.001	0.82
Filter feeder	0.48	1.11 ± 0.47	0.029	0.37	0.42 ± 0.09	<0.001	0.67
Invertebrate predator	0.56	1.03 ± 0.54	0.070	0.29	0.52 ± 0.11	<0.001	0.72
Fish	0.75	−0.07 ± 0.59	0.904	0.00	0.62 ± 0.13	<0.001	0.77

Notes: Algal δ^{13}C values were inferred from epilithic algal δ^{13}C, and from herbivore δ^{13}C when algae data were not available (AH δ^{13}C). For analyses of scraper data, only epilithic algae δ^{13}C were used to represent algal δ^{13}C. For analyses of collector data, scraper δ^{13}C were used instead of herbivore δ^{13}C to infer algal δ^{13}C because herbivore data sometimes included data for collectors. ''Coefficient'' indicates the standard partial regression coefficients from the multiple regression analyses, and error terms are ± 1 SE; ''r_{TD}'' and ''r_{AH}'' represent part correlation values of terrestrial or algal carbon sources, respectively, and consumer δ^{13}C. Part correlations show the influence of adding terrestrial or algal carbon sources to a regression model after accounting for the relationship of the other independent variable to consumer δ^{13}C.

† Regression results for shredders were strongly influenced by an outlier site (i.e., Site 35). Removing this site from the analysis improved the whole-model r^2 to 0.82.

streams and rivers. Relatively little data for epilithic algal δ^{13}C in small headwater streams (<10 km^2 watershed area) were available, so this relationship could not be evaluated in these habitats. However, algal δ^{13}C were distinct from terrestrial δ^{13}C in headwater streams, and algae were clearly not important to the diets of most consumers at these sites, suggesting that potential deviations in small streams from the relationship between algal and herbivore δ^{13}C observed in larger streams and rivers (i.e., Fig. 3) would not strongly influence the overall results of the regression analyses.

The third assumption was that terrestrial and algal δ^{13}C varied independently. For the sites used in the multiple regression analyses, linear regression of terrestrial and AH δ^{13}C showed that there was no relationship between the independent variables (coefficient $= 0.01$, $r^2 = 0.01$). At 4 out of 30 sites, the difference between terrestrial and AH δ^{13}C was $<2‰$; for these sites, the multiple regression analyses would not clearly distinguish between the importance of algal and terrestrial carbon sources in explaining consumer δ^{13}C. However, large differences in part correlation values for terrestrial and algal carbon sources and consumer δ^{13}C (Table 2) indicate that the influence of these sites on the overall analysis was minimal.

DISCUSSION

The observed variation in algal δ^{13}C with watershed area is important for at least three reasons. First, increases of algal δ^{13}C with watershed area are consistent with decreasing $CO_{2(aq)}$ and increasing photosynthesis rates often observed as stream size increases, and suggests that carbon limitation decreases fractionation of stable-carbon isotopes by algae in productive rivers. Second, the patterns of algal δ^{13}C confirm that in many headwater streams, stable-carbon-isotope ratios of algal and terrestrial production are distinct and may be used to distinguish the contribution of these carbon sources to stream food webs. Finally, patterns in consumer δ^{13}C suggest the importance of algal production to food webs in all but the smallest headwater streams. These three results are discussed separately below.

Controls of algal δ^{13}C

The pattern of algal ^{13}C-enrichment with watershed area suggests that effects of carbon limitation reduce discrimination against ^{13}C in more productive streams and rivers. I present two lines of evidence to support this hypothesis. First, strong downstream changes in resource availability and other environmental conditions within watersheds provide indirect evidence for the role of carbon limitation. Concentrations of $CO_{2(aq)}$ consistently decrease downstream due to reduced groundwater inputs relative to streamwater volume, increased water temperatures, and increased photosynthetic demand for $CO_{2(aq)}$ (Howard et al. 1984, Dawson et al. 1995, Jones and Mulholland 1998, Finlay et al. 1999). Primary production rates are positively related

to light intensity and temperature, and thus increase with watershed area, since canopy cover decreases and water temperature increases as stream channels widen (Lamberti and Steinman 1997). As a consequence, algal demand for $CO_{2(aq)}$ increases downstream, while concentration decreases. Limited $CO_{2(aq)}$ supply relative to demand (i.e., carbon limitation) increases algal δ^{13}C through reduced discrimination against ^{13}C when the entire pool of available $CO_{2(aq)}$ is used (Calder and Parker 1973, Pardue et al. 1976), and through decreased enzymatic fractionation of carbon isotopes, increased use of bicarbonate, or induction of carbon-concentrating mechanisms (Keeley and Sandquist 1992).

Second, while algal δ^{13}C were strongly related to δ^{13}C DIC (Fig. 5), there was no significant increase in δ^{13}C DIC with increasing watershed area. Warmer temperatures in open-canopied rivers would reduce the equilibrium fractionation between HCO_3^{-1} and $CO_{2(aq)}$ by 1–3‰ (Mook et al. 1974) and thus increase δ^{13}C $CO_{2(aq)}$ by up to 3‰. Increases in algal δ^{13}C were much greater than the potential equilibrium increases in δ^{13}C $CO_{2(aq)}$ (Fig. 2).

Confirmation of the importance of carbon limitation effects on algal δ^{13}C is provided by several recent field studies. In an unshaded headwater stream and Arctic river with relatively high $CO_{2(aq)}$, experimentally increased photosynthetic rates enriched algal δ^{13}C (MacLeod and Barton 1998 and Peterson et al. 1993, respectively). In another recent study, algal δ^{13}C in three closed-canopied tributary streams with high $CO_{2(aq)}$ were highly depleted relative to δ^{13}C DIC. By contrast, in three larger open-canopied rivers with low $CO_{2(aq)}$, algal δ^{13}C were high relative to δ^{13}C DIC (Finlay et al. 1999, δ^{13}C DIC data in Fig. 5). Furthermore, within the open-canopied rivers, pool algae were strongly ^{13}C-enriched relative to riffle algae, due to increased boundary layer effects on $CO_{2(aq)}$ supply in pools (Finlay et al. 1999).

An alternate hypothesis to explain spatial variation in algal δ^{13}C is that downstream changes in the biogeochemistry of inorganic carbon increase δ^{13}C $CO_{2(aq)}$ with watershed area. Under equilibrium conditions, δ^{13}C $CO_{2(aq)}$ should be directly related to δ^{13}C HCO_3^{-1}, the dominant form of DIC present at all sites examined. However, if $CO_{2(aq)}$ and HCO_3^{-1} are not in isotopic equilibrium, it is likely that δ^{13}C $CO_{2(aq)}$ could become more ^{13}C-enriched in productive rivers due to decreases in $CO_{2(aq)}$, leading to increased invasion of atmospheric CO_2 (e.g., Schindler et al. 1972).

However, distinguishing the relative importance of the two hypothesized controls of algal δ^{13}C is complex because of the correlations among many of the potential controls of algal δ^{13}C. For example, $CO_{2(aq)}$, an important determinant of carbon limitation effects on algal δ^{13}C, and δ^{13}C DIC should be negatively correlated because $CO_{2(aq)}$ in excess of atmospheric levels may be increasingly of heterotrophic origin. Further, many of the other factors that may influence algal photosynthe-

sis rates, such as light and temperature, may be correlated with $CO_{2(aq)}$. These examples demonstrate the need for experiments and observations from a wider range of environmental conditions to understand the controls of algal δ^{13}C in lotic ecosystems.

While the relative importance of the two hypothesized controls of algal δ^{13}C is currently unresolved, the dominant controls of algal δ^{13}C should change with stream productivity and size. In shaded headwater streams, spatial and temporal variation in δ^{13}C $CO_{2(aq)}$, due to variation in groundwater inputs, stream geomorphology, and weathering reactions in terrestrial ecosystems (Kendall et al. 1992, Jones and Mulholland 1998), may be the dominant influence on algal δ^{13}C. In contrast, algal δ^{13}C in productive streams or rivers may be more strongly determined by effects of carbon limitation than changes in CO_2 sources. While fewer data are available from larger rivers (i.e., $>$4000-km^2 watershed area), benthic algal δ^{13}C should become depleted further downstream relative to mid-order reaches because of decreased algal productivity due to turbidity and increasing $CO_{2(aq)}$ from heterotrophic respiration (Vannote et al. 1980). Consumer δ^{13}C should also become depleted downstream due to the isotopic depletion of benthic algae as described above, or the increasing trophic importance of phytoplankton or terrestrial detritus (Vannote et al. 1980, Araujo-Lima et al. 1986, Hamilton et al. 1992).

Implications for determining the trophic basis of production in river food webs

Stable-carbon-isotope analyses have been frequently used to assess the contribution of terrestrial detritus and algal production to stream food webs (Rounick and Winterbourn 1986). The analyses presented here show that in shaded headwater streams, epilithic algal δ^{13}C are often highly distinct from terrestrial detritus δ^{13}C. These analyses may be conservative if herbivore δ^{13}C, used to infer algal δ^{13}C in many cases, were increased by trophic effects or by consumption of terrestrial detritus. Thus, measurements of consumer δ^{13}C may provide a means to quantify algal and terrestrial contributions to many headwater stream food webs provided that the following three assumptions are met. First, the factors that influence fractionation of stable-carbon isotopes by algae, such as carbon supply and photosynthetic rates, must not be spatially variable over the study area. Since shaded tributary streams are often characterized by supersaturated $CO_{2(aq)}$ and low rates of primary productivity, carbon limitation effects on algal δ^{13}C may often be minimal in these habitats. Second, $CO_{2(aq)}$ sources with different δ^{13}C must not be spatially variable over the study site or reach. In areas of large groundwater contributions to streamflow, such as in upwelling zones and springs (Rounick and James 1984), δ^{13}C $CO_{2(aq)}$ may change rapidly due to inputs of isotopically light respiratory CO_2. Measurements of $CO_{2(aq)}$ would provide an indicator of potential spatial

variability of δ^{13}C $CO_{2(aq)}$. Finally, epilithic algal carbon must be adequately separated from other material for measurement of algal δ^{13}C endpoints. These measurements can be made by thorough dissection of samples, or through compound-specific δ^{13}C analyses (e.g., Hamilton et al. 1992, Sachs et al. 1999).

The degree to which terrestrial and algal δ^{13}C are distinct will also depend on the values of terrestrial detritus that best represent available terrestrially derived carbon sources to stream heterotrophs and macroinvertebrate consumers, since foliar δ^{13}C were significantly ^{13}C-depleted relative to CPOM and FPOM. Enrichment in leaf litter appears to occur at or soon after leaf abscission (e.g., Rounick et al. 1982, Schiff et al. 1997), suggesting that conditioned leaf δ^{13}C may be a better measure of terrestrial inputs to streams than foliar δ^{13}C. Furthermore, conditioned leaf litter is often preferred to fresh litter by stream consumers (Allan 1995). Additional enrichment of organic matter δ^{13}C may occur during decomposition due to preferential microbial use of ^{12}C during decomposition (Nadelhoffer and Fry 1988), as indicated by increased FPOM and DOC δ^{13}C relative to CPOM δ^{13}C. Fewer data were available for DOC, an important terrestrially derived carbon source for heterotrophs in many headwater streams. Schiff et al. (1997) showed that DOC δ^{13}C in stream and groundwater were most similar to leaf litter on the soil surface, and DOC δ^{13}C were very similar to FPOM and CPOM δ^{13}C in this study. Thus, the limited evidence available suggests that terrestrial detritus δ^{13}C in streams are best represented by senesced or conditioned leaves and not live foliage.

In some unshaded, productive rivers, measurement of consumer δ^{13}C may be less useful in distinguishing the importance of terrestrial vs. algal carbon sources due to the overlap in terrestrial and algal δ^{13}C. Perhaps more important, however, effects of carbon limitation may cause algal δ^{13}C to vary with $CO_{2(aq)}$ supply (Finlay et al. 1999) or algal productivity (Peterson et al. 1993, MacLeod and Barton 1998), providing a natural tracer of algal production derived from distinct habitats or reaches through river food webs.

The importance of algal production to river food webs

Downstream trends in algal and consumer δ^{13}C with watershed area, and multiple regression analyses of terrestrial and algal carbon sources and consumer δ^{13}C, suggest reliance on algal production by higher trophic levels in many stream food webs. Small headwater streams ($<$10 km^2 watershed area) were an exception. In these streams, most consumer groups relied primarily on inputs of terrestrial carbon consistent with the River Continuum Concept (RCC) descriptive model of energy flow in streams (Vannote et al. 1980) and results of experimental studies in temperate forested watersheds (e.g., Wallace et al. 1997). In such headwater stream ecosystems, low algal productivity and

high inputs and retention of terrestrial detritus may reduce the relative importance of algae to higher trophic levels. However, algal production was clearly important to diets of scrapers at all headwater sites where scrapers were present, and to collectors and filter feeders at some sites.

In streams and rivers in watersheds >10 km^2, consumer δ^{13}C were more strongly related to algal than terrestrial carbon sources for all groups except shredders (Table 2), even though most organic matter in rivers is terrestrially derived. Measurements of CPOM and FPOM δ^{13}C reported here demonstrate the terrestrial origin of benthic organic matter, confirming previous research (summarized in Webster and Meyer 1997) showing that terrestrial carbon sources dominate the benthic standing stocks and fluxes of organic carbon in most temperate rivers. Such observations of low abundance of benthic algae relative to terrestrial organic matter strongly influenced the RCC, which predicts the dominance of terrestrial sources as the energy base for food webs in headwater streams, and a transition to terrestrial and algal carbon sources in midordered rivers (Vannote et al. 1980). My results suggest that the transition from reliance on terrestrial detritus to reliance on algae by consumers occurs as algal primary production increases in watersheds ≥10 km^2, although contributions of algae and terrestrial detritus often vary between functional feeding groups at the same site. Detrital food webs appear to be largely decoupled from production at higher trophic levels in many downstream sites, possibly due to the low quality of terrestrial organic carbon relative to algae. This suggestion is consistent with the conclusions of several stable-isotope-based studies of rivers where algal biomass represented a small percentage of the available pool of organic matter, but appeared to be the most important energy source to higher trophic levels (Araujo-Lima et al. 1986, Hamilton et al. 1992, Peterson et al. 1993, Thorp et al. 1998).

However, in some streams, terrestrial inputs are clearly important to the energy base of consumers, and the mechanisms responsible for between-site differences in terrestrial and algal contributions to food webs in streams of similar sizes remain poorly understood. Potential controls of the relative importance of terrestrial vs. algal carbon to stream food webs include variation in the quality or amount of terrestrial inputs or algal production, and variation in the abundance of particular functional feeding groups. Measurements of the availability of algal and detrital resources and abundance of invertebrates, (rarely reported in stable-carbon-isotope studies) used in conjunction with stable-isotope methods, would add considerably to understanding the relative importance of terrestrial vs. algal production to energy flow through stream food webs.

Clearly, the contribution of algal and terrestrial carbon sources to stream food webs cannot be completely quantified with previously published stable carbon iso-

tope data alone due to the overlap in algal and terrestrial δ^{13}C in some larger streams and rivers, and the limited number of direct measurements of algal δ^{13}C in headwater streams. However, use of other natural tracers such as δ^{15}N, and improved methods for algal δ^{13}C analysis, should greatly enhance the use of stable isotope measurements to understand energy flow through river food webs.

Conclusions

The analyses of patterns in algal δ^{13}C presented here reveal the importance of algal production to almost all river and stream food webs studied, and provide a spatial context for the use of natural variation in stable-carbon isotopes to distinguish algal and terrestrial carbon sources to food webs in lotic ecosystems. Future research efforts should focus on measurements of algal δ^{13}C, particularly in headwater streams, where algae may be disproportionately (in terms of biomass) more important for higher trophic levels than terrestrial detritus, and where stable-carbon isotopes are clearly able to distinguish potential carbon sources for stream food webs. However, measurements of stable-carbon-isotope ratios alone may not distinguish terrestrial and algal production in productive streams and rivers because of overlap in δ^{13}C values and variation of algal δ^{13}C at small spatial scales. At present, stable-carbon-isotope measurements are powerful food web and ecosystem tracers, and the full potential for this methods remains to be realized with additional investigation of the controls of algal δ^{13}C.

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