

## Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies

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### Abstract

We used variation in algal  $\delta^{13}\text{C}$  between river habitats to study the spatial scale of energy flow through river food webs. We found a strong negative relationship between herbivore  $\delta^{13}\text{C}$  (which reflects algal  $\delta^{13}\text{C}$ ) and water velocity in three productive Northern California rivers but not in unproductive streams. The contrast among habitats suggests that water velocity affects algal  $\delta^{13}\text{C}$  most strongly when  $\text{CO}_2$  availability is low relative to photosynthetic rates. Our results help explain the wide variation in published river biota  $\delta^{13}\text{C}$  and show that past studies using carbon isotope analyses may have significantly underestimated the importance of algal-derived carbon to river food webs. While flow-related variation in  $\delta^{13}\text{C}$  complicates this common application of carbon isotope analysis, we show that it provides a natural tracer of the flux of algal production derived from different habitats within rivers to higher trophic levels. Measurements of consumer  $\delta^{13}\text{C}$  showed that most invertebrate and vertebrate consumers relied on local production, except for filter-feeding insects and steelhead trout, which relied on production derived from multiple sources. Stable carbon isotopes may thus be used to spatially delineate the habitats that support river food webs, providing previously unavailable information for understanding and managing river ecosystems.

River food webs are based on both local microalgal production and carbon transported from terrestrial or upstream aquatic ecosystems. Determining the sources of production for river food webs is a major challenge to river ecologists because of the complexity of controls over carbon sources and the mobility of consumers (Schlosser 1991; Cummins et al. 1995). Stable carbon isotopes ( $^{13}\text{C}/^{12}\text{C}$  or  $\delta^{13}\text{C}$ ) hold much promise as a tool for determining the energy base of river and stream food webs because terrestrial and aquatic plants often have different ratios of stable carbon isotopes (Rounick and Winterbourn 1986), and there is relatively small isotopic fractionation associated with trophic transfer of organic carbon (DeNiro and Epstein 1978; France 1996a). Use of carbon isotopes in streams and rivers, however, has been limited by unexplained variability in autotrophic  $\delta^{13}\text{C}$  (France 1995, 1996b, but see Doucett et al. 1996a). Some of the variability in algal  $\delta^{13}\text{C}$  has been attributed to the different isotopic signatures of the dissolved inorganic carbon (DIC) available to aquatic plants (i.e., atmospheric  $\text{CO}_2$ , biogenic  $\text{CO}_2$ , and weathered bicarbonate) (Rounick and James 1984), but this mechanism cannot account for the large magnitude of variation often observed within rivers. In ocean or lake ecosystems, algal  $\delta^{13}\text{C}$  values are often determined by the relative supply and demand for  $\text{CO}_2$  by autotrophs (Hecky and Hesslein 1995; Fry 1996; Schindler et al. 1997). However, stable carbon isotope studies of river and

stream food webs have rarely considered the role of these factors in determining algal carbon isotope ratios.

In six northern California streams and rivers that varied in algal biomass and primary production (Table 1), we examined the effect of  $\text{CO}_2$  supply on microalgal (predominantly diatom) carbon isotope ratios. We inferred variation in  $\text{CO}_2$  supply to benthic algae within sites from measurement of current velocity above the substrate because current velocity strongly affects the thickness of the boundary layer around benthic organisms. Because of the slow diffusion of  $\text{CO}_2$  in water, boundary layer thickness strongly influences the supply rate of  $\text{CO}_2$  to algae (Keeley and Sandquist 1992). When  $\text{CO}_2$  concentrations are depleted in the boundary layer around benthic algae, effects of carbon limitation result in enriched algal  $\delta^{13}\text{C}$  (Keeley and Sandquist 1992; Hecky and Hesslein 1995).

The study was conducted near the forested headwaters of the South Fork Eel River in Mendocino County, California (39°44'N, 123°39'W). Most precipitation falls between October and May, and discharge declines steadily after winter floods to stable summer baseflows. The three largest rivers have wide channels and sunlit streambeds, low turbidity and dissolved color, and they are highly productive during summer baseflows (Power 1990, unpubl. data). Physical and chemical conditions were similar from May through October 1997 (Finlay unpubl. data), allowing adequate time for biomass of the benthic invertebrates and juvenile fishes sampled to reach isotopic equilibrium with their food sources.

Benthic substrate type (i.e., epilithic, detrital, or algal filaments longer than 3 cm) was determined with point transects in pool and riffle habitats; epilithic algal biomass on rocks without filamentous algae was measured by removing algae from known areas of cobbles with a wire brush and determining total chlorophyll *a* (Chl *a*) concentrations fluorometrically following extraction in 90% acetone. Canopy cover was estimated by spherical densitometry.  $\text{CO}_2$  was measured by equilibrating well-mixed river water with ambient atmospheric air in a plastic syringe. Following equi-

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Table 1. Physical, chemical, and biological characteristics of the study streams and rivers in 1997. The gradient of small streams to midsized rivers encompassed much of the physical and chemical variability present in past applications of carbon isotope analyses to study of lotic food webs. Filamentous algae (mostly *Cladophora*) were present only in Ten Mile Creek (40% cover) and the South Fork Eel River (25% cover). Error terms are  $\pm 1$  SE. All data except drainage area are means for the month of July.

River/ Stream	Drainage area (km <sup>2</sup> )	Discharge (liter s <sup>-1</sup> )	Water temperature (°C)	Canopy cover (%)	Epilithic Chl <i>a</i> ( $\mu\text{g cm}^{-2}$ )	pH		CO <sub>2</sub> ( $\mu\text{M}$ )	
						Day	Night	Day	Night
Ten Mile	180	No data	23.6	6.9 ( $\pm 3$ )	0.96 ( $\pm 0.21$ )	8.7	No data	No data	No data
Eel	130	995	22.5	39.1 ( $\pm 12$ )	3.36 ( $\pm 0.77$ )	8.5	7.7	9.7	19.9
Elder	16.8	99.1	16.7	86.1 ( $\pm 8$ )	2.24 ( $\pm 0.68$ )	8.1	7.7	11.4	25.2
Fox	2.6	10.8	15.3	97.5 ( $\pm 3$ )	0.47 ( $\pm 0.08$ )	7.9	7.7	45.4	41.3
Skunk	1.4	0.7	13.6	97.0 ( $\pm 3$ )	0.48 ( $\pm 0.49$ )	7.6	7.6	41.8	40.8
McKinley	1.0	0.2	15.1	98.1 ( $\pm 2$ )	0.21 ( $\pm 0.15$ )	7.5	7.4	142.1	138.1

bration, the syringe headspace was transferred to a gastight nylon syringe and analyzed with an infrared gas analyzer within 24 h.

We used herbivores to measure the effect of current on 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. This approach may have introduced two forms of additional complexity into our analyses of water velocity effects on algal  $\delta^{13}C$  and our subsequent food-web analyses. First, trophic transfer of organic carbon is associated with isotopic enrichment of the consumer by about 1‰ (DeNiro and Epstein 1978; France 1996a). Given the high levels of variability in algal  $\delta^{13}C$  in rivers and the potential mobility of invertebrate herbivores, we did not attempt to assess the true fractionation between algae and herbivores in our field setting. However, we suggest that relative to other sources of algal  $\delta^{13}C$  variability, enrichment in herbivore  $\delta^{13}C$  relative to algae represents a small source of error in our analyses.

The second possible complexity introduced by using herbivore  $\delta^{13}C$  to infer algal  $\delta^{13}C$  is the potential consumption of terrestrial detritus by herbivores, because assimilation of terrestrial organic matter would substantially alter herbivore

$\delta^{13}C$  in some cases. Further, assimilation of terrestrial detritus would complicate food-web analyses because algal and detrital  $\delta^{13}C$  may overlap. We believe that terrestrial detritus played a minor role in herbivore diets in the three productive rivers and present three lines of indirect evidence to support this. First, abundance of terrestrial detritus was extremely low in productive rivers, covering <3% of the riverbed in all three cases. Second, concentrations of dissolved organic carbon (DOC) were low at all sites (ca. 1 mg liter<sup>-1</sup>, Finlay unpubl. data), probably due to the lack of wetlands in the watershed and absence of summer rain, which would flush terrestrial DOC from the soil. Finally, carbon isotope analysis of epilithic diatoms scraped from pool and riffle rocks in the three productive rivers confirmed that invertebrate carbon isotope ratios were similar to the isotope ratios of their algal foods (Table 2). Similar measurements of algal  $\delta^{13}C$  from epilithic diatoms could not be obtained from the small tributary streams because it was not possible to adequately separate epilithic algae from heterotrophs and detritus. In the tributary streams, where abundance of terrestrial detritus was greater, herbivore  $\delta^{13}C$  values may be less accurate indicators of algal  $\delta^{13}C$ . However, the high quality of algal carbon may make algae more important to herbivore diets than suggested

Table 2. Average epilithic algae and herbivore  $\delta^{13}C$  in pool and riffle habitats in July 1997. The depleted value of riffle herbivores relative to algae in Ten Mile Creek was due to the inclusion of data for Blepharicerid larvae ( $-32.0\text{‰}$ ), which lived in the fastest flow environment; removing this datum from the mean estimation gave a value of  $-26.7\text{‰}$ , about 1‰ less than the average  $\delta^{13}C$  for algae. Differences between mean pool and riffle algae and herbivore  $\delta^{13}C$  were significant (*t*-tests,  $P < 0.05$ ) only in productive rivers (i.e., Eel River, Elder Creek, and Ten Mile Creek). Pure samples of epilithic algae could not be obtained from tributary streams.

River/Stream	Trophic group	Pool			Riffle		
		$\delta^{13}C$	$\pm$ SE	<i>n</i>	$\delta^{13}C$	$\pm$ SE	<i>n</i>
Productive rivers							
Ten Mile	Epilithic algae	-20.7	0.1	3	-25.6	1.1	2
	Invertebrate herbivores	-20.4	0.8	9	-28.1	1.5	4
Eel	Epilithic algae	-17.9	0.7	10	-26.2	0.7	8
	Invertebrate herbivores	-18.2	0.6	23	-25.3	0.9	12
Elder	Epilithic algae	-21.7	0.4	10	-27.5	0.5	10
	Invertebrate herbivores	-20.4	0.5	14	-25.4	0.9	8
Unproductive tributary streams							
Fox	Invertebrate herbivores	-31.5	1.3	5	-30.1	0.8	7
Skunk and McKinley	Invertebrate herbivores	-32.8	0.9	5	-34.4	1.7	5

by its low abundance relative to detritus (e.g., Mayer and Likens 1987; Hamilton et al. 1992; Peterson et al. 1993).

Different habitats (i.e., pools and riffles) of the six rivers and streams were sampled along continua of current velocities in July 1997. The gradient of small streams to midsized rivers encompassed much of the physical and chemical variability in other investigations where carbon isotope analyses have been used to study lotic food webs. Two or three pool-riffle pairs were sampled in each river, and at each site, samples were usually collected from areas of the stream no more than 10 m apart to minimize potential bulk water differences in  $\delta^{13}\text{C}$  of DIC available to benthic algae. Samples of 2–30 invertebrate larvae from one to three adjacent diatom-covered cobbles or filamentous algal mats were collected and composited for each sample. Current velocity was measured approximately 6 cm above the sampled substrata with an electromagnetic Marsh–McBirney flowmeter (model 2000); we did not attempt to measure the flow rate at the exact location of individual herbivores. To reduce potential variability associated with heterogeneous current velocities around individual cobbles, we composited many individual herbivores for each sample. At each site, samples were collected of the most abundant species. Herbivores sampled were primarily Ephemeroptera (*Timpanoga* sp., *Nixe* sp., *Epeorus* sp., and *Seratella* sp.) and Trichoptera (*Dicosmoecus gilvipes*, *Gumaga* sp., *Neophylax* spp., *Glossosoma* spp., and *Psychoglypha* sp.) larvae. Blepharicerid larvae (Diptera) were also sampled from fast-flowing areas of riffles in Ten Mile Creek and the Eel River, and Coleoptera larvae (*Eubrianax* sp.) were collected from several sites in Elder and Fox Creeks. *Dicosmoecus*, *Neophylax*, *Glossosoma*, *Eubrianax*, and Blepharicerid larvae are scrapers; other taxa are generalist collectors. Obligate Trichopteran shredders (*Lepidostoma* sp. and *Heteroplectron* sp.) were sampled from deposits of terrestrial detritus (i.e., leaves or woody debris). *Lepidostoma* was also sampled from epilithic habitats. Invertebrate predators sampled were primarily Odonata (*Aeshna californica*), Plecoptera (*Calineuria californica* and *Hesperoperla pacifica*), and Hemiptera (*Ambrysus mormon*) larvae.

Insect guts were removed within several hours of collection by dissection and discarded. Samples were dried at 55°C for 48 h. Dried invertebrates, epilithic diatoms scraped from rocks, and muscle and scale tissue collected from vertebrate predators were ground to a powder before stable carbon and nitrogen ( $^{15}\text{N}/^{14}\text{N}$  or  $\delta^{15}\text{N}$ ) isotope analyses on a Europa 20-20 continuous flow mass spectrometer.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are expressed relative to the PeeDee Belemnite standard and the atmospheric nitrogen standard, respectively. The average standard deviation for 37 samples of algae and consumers run in duplicate was 0.14 and 0.16‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. We did not extract lipids from invertebrate samples because we did not expect differences in lipid content between pools and riffle herbivores. Regression analyses of carbon to nitrogen ratios (C/N) of herbivores, an indicator of lipid content (McConnaughey and McRoy 1979), showed no effect of water velocity on C/N and no relationship between C/N and herbivore  $\delta^{13}\text{C}$  (Finlay unpubl. data).

Average herbivore  $\delta^{13}\text{C}$  values in pool and riffle habitats were calculated by assigning laminar flows of  $<0.25\text{ m s}^{-1}$

as “pools” and turbulent flows (usually  $>0.3\text{ m s}^{-1}$ ) as “riffles.” Herbivores were collected from depths of 5–50 cm in pools and riffles. Data for McKinley and Skunk Creeks were combined because of small sample sizes in fast- and slow-flow environments, respectively; physical characteristics were similar for these streams (Table 1). Regression analyses of herbivore  $\delta^{13}\text{C}$  against current velocity used data from organisms collected from epilithic surfaces and did not discriminate between scrapers or generalist collector invertebrates. For a given current velocity in productive rivers, there was no consistent difference between  $\delta^{13}\text{C}$  of these groups (Finlay unpubl. data). Data from invertebrates collected from terrestrial detritus were not included in regression analyses.

Epilithic surfaces were the most common substrata in the three productive rivers. Point transect surveys showed that deposits of terrestrial detritus covered  $<3\%$  of the benthic habitats in these rivers but covered between 5 and 20% of the stream bottom in tributaries.

Detritivorous Trichoptera larvae (*Lepidostoma* sp. and *Heteroplectron* sp.) sampled from deposits of detritus had an average  $\delta^{13}\text{C}$  value of  $-26.4\text{‰} \pm 0.1$  ( $\pm\text{SE}$ ,  $n = 35$ ) in tributary streams and rivers. Detritivore  $\delta^{13}\text{C}$  values were enriched by about 1‰ compared to average  $\delta^{13}\text{C}$  values of  $-27.5\text{‰} \pm 0.2$  ( $n = 6$ ) for coarse particulate organic matter sampled from tributary streams. *Lepidostoma* sampled from epilithic habitats in flows of  $0.0\text{--}0.06\text{ m s}^{-1}$  in early August had enriched  $\delta^{13}\text{C}$  in the Eel River ( $-17.2\text{‰} \pm 1.0$ ,  $n = 2$ ) and Elder Creek ( $-17.6\text{‰} \pm 1.1$ ,  $n = 2$ ). Although considered to be primarily shredders, epilithic *Lepidostoma*  $\delta^{13}\text{C}$  were more similar to pool algae (Table 2) than terrestrial detritus (i.e.,  $-27.5\text{‰}$ ). Obligate detritivores were not sampled from epilithic habitats in other streams and rivers. Invertebrate herbivores sampled from tributary streams had depleted  $\delta^{13}\text{C}$  relative to detritivores ( $t$ -tests,  $P < 0.05$  in all cases; Table 2), indicating that even in streams where terrestrial detritus was abundant, epilithic diatoms were a significant carbon source for the herbivorous species sampled.

Both epilithic algae and herbivore  $\delta^{13}\text{C}$  were enriched by an average of 5–8‰ in pools compared to riffles in productive rivers (Elder, South Fork Eel, Ten Mile; Table 2). Furthermore, herbivore data suggested continuous depletion in algal  $\delta^{13}\text{C}$  with increasing current velocity (Fig. 1). Blepharicerid larvae, which attach to the tops of rocks in the fastest flows with suction disks and graze algae (Courtney et al. 1996), were  $^{13}\text{C}$  depleted relative to other riffle herbivores in Ten Mile Creek and the South Fork Eel River ( $-32.0$  and  $-31.1\text{‰}$ , respectively), indicating that the maximum carbon isotope fractionation by benthic algae occurred in stream habitats where  $\text{CO}_2$  supply rate (i.e., current velocity) was highest.

Water stagnation in pools may have caused the variability in algal  $\delta^{13}\text{C}$  observed at low current velocities in productive rivers (Fig. 1). The most enriched herbivore  $\delta^{13}\text{C}$  values were always observed in samples collected at pool edges where water exchange with the main channel was reduced, resulting in increased water temperatures (Finlay unpubl. data). Our method of measuring current velocity was insensitive at the low flows encountered at pool edges ( $<5\text{ cm s}^{-1}$ ). However, water stagnation could enrich algal  $\delta^{13}\text{C}$  through both

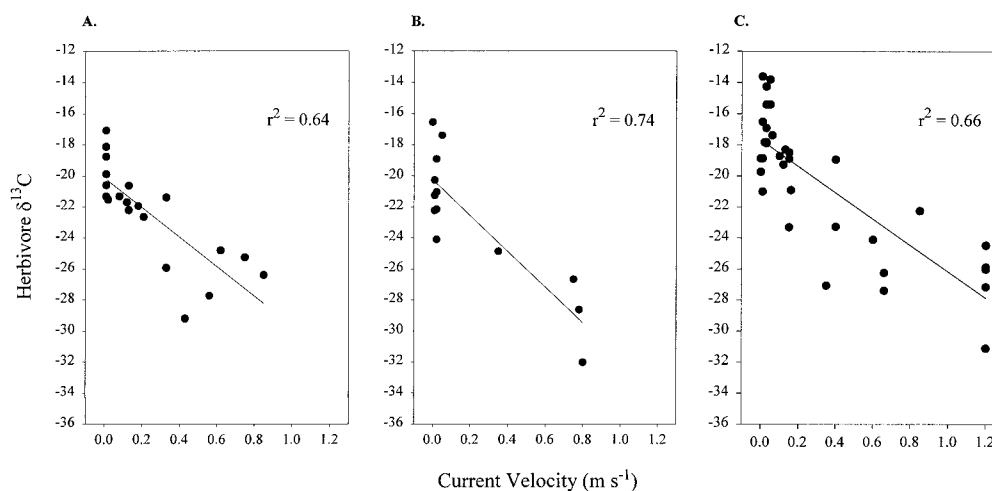


Fig. 1. Relationship of current velocity with herbivore  $\delta^{13}\text{C}$  in productive rivers in 1997: (A) Elder, (B) Ten Mile, and (C) South Fork Eel. Herbivore  $\delta^{13}\text{C}$  data for invertebrates sampled from cobbles (i.e., not from filamentous algae) are presented. Slopes for linear regression models were significant in each case ( $t$ -tests,  $P < 0.001$ ). Regression slopes for similar relationships in smaller tributary streams (data not shown) were not significant ( $t$ -tests,  $P > 0.05$ ).

boundary layer effects and low  $\text{CO}_2$  concentrations caused by warm water temperatures.

In contrast to productive rivers, current velocity did not affect algal  $\delta^{13}\text{C}$  in the unproductive tributary streams (Fox, McKinley, Skunk; Fig. 1; Table 2), suggesting that  $\text{CO}_2$  availability relative to rates of primary production determines current velocity effects on algal carbon isotope ratios. High daytime pH values and low dissolved  $\text{CO}_2$  concentrations (Table 1) in productive relative to unproductive streams indicated that  $\text{CO}_2$  availability was lowest in rivers with the greatest algal biomass. Daytime  $\text{CO}_2$  levels were at least four times greater in the heavily shaded tributary streams with low algal biomass than in the South Fork Eel River and Elder Creek, indicating a relatively low photosynthetic demand for inorganic carbon. Only in rivers with high insolation and algal biomass were photosynthesis-driven increases in pH large and decreases in  $\text{CO}_2$  significant ( $t$ -tests,  $P < 0.05$  in all cases; Table 1).

Current velocity effects on algal  $\delta^{13}\text{C}$  may be attributed to the increased supply rate of  $\text{CO}_2$  to benthic algae with increased water velocity because discrimination against  $^{13}\text{CO}_2$  during photosynthesis increases with  $\text{CO}_2$  availability (Calder and Parker 1973; Pardue et al. 1976). Plant physiologists have long noted that water velocity plays an important role in determining inorganic carbon availability and carbon isotope ratios of stream macrophytes and macroalgae (Keeley and Sandquist 1992), but water velocity effects have not been considered in previous carbon isotope studies of river food webs. In two other recent studies, algal  $\delta^{13}\text{C}$  was positively related to photosynthesis rates (Peterson et al. 1993; MacLeod and Barton 1998). One study of algal  $\delta^{13}\text{C}$  found no effect of water velocity on algal  $\delta^{13}\text{C}$  in a headwater stream with supersaturated levels of  $\text{CO}_2$  (MacLeod and Barton 1998). While the controls of algal  $\delta^{13}\text{C}$  in rivers are poorly understood, the evidence available suggests that, as observed in ocean (Fry 1996) and lake (Hecky and Hesslein 1995; Schindler et al. 1997) ecosystems, both supply and

demand for  $\text{CO}_2$  appear to have strong effects on algal  $\delta^{13}\text{C}$  in rivers. Given that water velocity not only affects inorganic carbon supply but also algal physiology and availability of nitrogen and phosphorus (Stevenson 1996), we expect that metabolism and velocity effects on algal  $\delta^{13}\text{C}$  are strongly interrelated.

Effects of carbon supply or photosynthetic demand on carbon isotope fractionation by benthic algae in streams may account for considerable unexplained variability in published producer and consumer  $\delta^{13}\text{C}$  values. For example, variation in the  $\delta^{13}\text{C}$  DIC among streams is often insufficient to explain variation in algal or herbivore  $\delta^{13}\text{C}$ , even in low pH environments where most DIC is present as  $\text{CO}_2$  (Rounick et al. 1982; Rounick and Hicks 1985; Junger and Planas 1994; Doucett et al. 1996b). Also, variation among herbivore species within sites is often on the order of 3–10‰ (Rounick et al. 1982; Rounick and Hicks 1985; Junger and Planas 1994; Doucett et al. 1996b). While some of this variation may be due to reliance on a mixture of terrestrial and algal carbon sources, within-site variation is often high even in strongly autotrophic river ecosystems (e.g., Junger and Planas 1994; Doucett et al. 1996b). Finally, herbivore species that graze in fast-flowing habitats usually have more negative values than other herbivores in the same reach (Rounick et al. 1982; Rounick and Hicks 1985).

Stream ecologists have most often used carbon isotope analyses to estimate the relative contribution of in-channel algal vs. terrestrial primary production to river food webs. At sites where algal and terrestrial organic matter have different  $\delta^{13}\text{C}$ , consumer  $\delta^{13}\text{C}$  has been used to estimate contributions of algal and terrestrial carbon to river food webs. Because current velocity effects on microalgal  $\delta^{13}\text{C}$  were previously unknown, these studies characterized algal carbon sources with a small number of samples without controlling for current velocity effects on algal  $\delta^{13}\text{C}$  in their analyses. Where flow effects were significant, we found up to 17‰ differences between herbivores sampled from adjacent pools

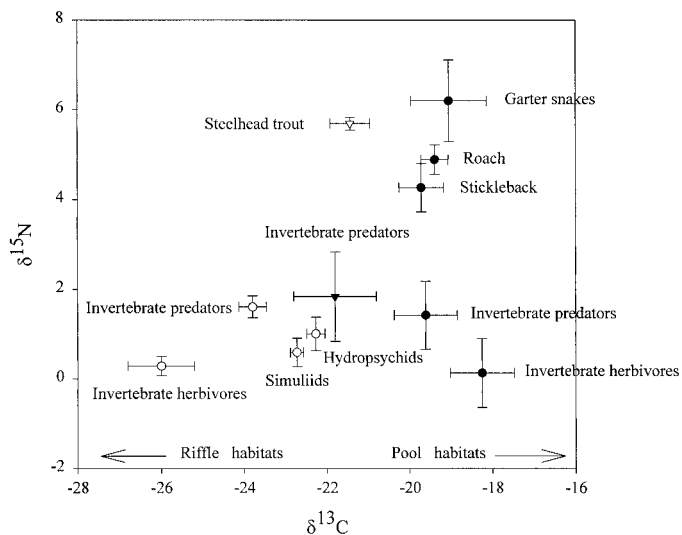


Fig. 2. Dual isotope plot of food webs in the two most similar productive rivers (South Fork Eel River and Ten Mile Creek). Nitrogen and carbon isotope data were averaged by habitat for samples collected in July 1997. Error bars represent  $\pm 1$  SE. Symbols represent invertebrates and vertebrates sampled from riffles (open circles), pools (closed circles), intermediate flows between 0.2 and 0.35  $\text{m s}^{-1}$  (closed triangles) and year 1–2 steelhead trout (open triangles). Steelhead trout (7–14 cm standard length) were sampled from pool and riffle habitats. Predatory invertebrates in intermediate flows were sampled from algal mats.

and riffles. This difference approaches the full range of variation of herbivore  $\delta^{13}\text{C}$  reported in the literature (i.e., 20‰; France 1995), suggesting that, in productive rivers, use of a single  $\delta^{13}\text{C}$  endpoint would not be sufficient to represent algal carbon sources. If variability in consumer  $\delta^{13}\text{C}$  attributed to reliance on terrestrial carbon was actually due to flow effects on algal  $\delta^{13}\text{C}$ , algal carbon contributions to river food webs would be substantially underestimated in many cases. At present, the degree to which flow has affected published  $\delta^{13}\text{C}$  values of stream biota cannot be adequately determined. Measurement of carbon chemistry, water velocity, and  $\delta^{13}\text{C}$  of DIC in future applications of carbon isotope analysis to food web studies should enhance prediction of where and when carbon isotope measurements will be useful in distinguishing the contributions of terrestrial and autotrophic production to river food webs.

Although carbon supply or metabolism effects on algal  $\delta^{13}\text{C}$  may complicate the most common previous use of carbon isotope analyses, we suggest that carbon isotope ratios will provide a tool for understanding the spatial scales of trophic interactions in productive rivers. We used current velocity effects on algal and herbivore  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to determine energy flow and trophic structure of food webs in the Eel River and Ten Mile Creek.  $\delta^{15}\text{N}$  values indicate trophic position in food webs because of consistent fractionation (by about 3.4‰) with each trophic transfer (Minagawa and Wada 1984; Kling et al. 1992; Cabana and Rasmussen 1994). A dual isotope plot of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  shows that most invertebrate predators in pool and riffle habitats largely depend on locally available prey (Fig. 2), consistent with the limited mobility and small foraging range of benthic inver-

tebrates. In contrast, filter-feeding simuliid and hydropsychid caddisfly larvae, which live in the fastest riffle flow environments, consumed invertebrate prey and organic matter transported from more lentic areas of the rivers. Pool-dwelling predators (garter snakes [*Thamnophis couchii*], three spined sticklebacks [*Gasterosteus aculeatus*], and a minnow [*Hesperoleucas symmetricus*]), were  $\delta^{13}\text{C}$  enriched, suggesting heavy reliance on prey derived from local pool primary production and not on production imported from faster flowing habitats. By contrast, highly mobile juvenile steelhead trout (*Oncorhynchus mykiss*) had enriched  $\delta^{15}\text{N}$  and intermediate  $\delta^{13}\text{C}$ , indicating that this top predator relied heavily on predatory invertebrates and *Hesperoleucas* derived either from areas of the river with intermediate current velocities or from a mix of pool and riffle habitats. We suggest that terrestrial detritus played a minor role in these food web results because of the low abundance of terrestrial detritus in the rivers and the low levels of DOC in stream and river water. To fully explore the potential complexity of these food webs, we are currently measuring the seasonal patterns of stable isotope ratios of invertebrate prey, organic matter sources, and long-lived vertebrate predators. However, the preliminary results presented here show that carbon isotope analysis can reveal the spatial scales of trophic interactions in rivers that are determined by the mobility of both predators and prey.

A fundamental tenet of river ecology is that upstream habitats are trophically connected to downstream reaches via the transport of organic matter and nutrients (Vannote et al. 1980). Natural variation of algal  $\delta^{13}\text{C}$  with current velocity or with algal productivity (Peterson et al. 1993) provides a tool to delineate the spatial scales of these transport processes and to examine the role of predator and prey mobility in determining trophic connections between adjacent river habitats. Isotopic distinction of production between habitats should also be useful in determining effects on river food webs of human alteration of habitat structure or flow regime by dams, diversions, or channelization.

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