Ecology, 83(7), 2002, pp. 1845–1859

SPATIAL SCALES OF CARBON FLOW IN A RIVER FOOD WEB

JACQUES C. FINLAY,[1] SAPNA KHANDWALA,[2] AND MARY E. POWER

Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA

Abstract. Spatial extents of food webs that support stream and river consumers are largely unknown, but such information is essential for basic understanding and management of lotic ecosystems. We used predictable variation in algal $\delta^{13}C$ with water velocity, and measurements of consumer $\delta^{13}C$ and $\delta^{15}N$ to examine carbon flow and trophic structure in food webs of the South Fork Eel River in Northern California. Analyses of $\delta^{13}C$ showed that the most abundant macroinvertebrate groups (collector-gatherers and scrapers) relied on algae from local sources within their riffle or shallow pool habitats. In contrast, filter-feeding invertebrates in riffles relied in part on algal production derived from upstream shallow pools. Riffle invertebrate predators also relied in part on consumers of pool-derived algal carbon. One abundant taxon drifting from shallow pools and riffles (baetid mayflies) relied on algal production derived from the habitats from which they dispersed. The trophic linkage from pool algae to riffle invertebrate predators was thus mediated through either predation on pool herbivores dispersing into riffles, or on filter feeders.

Algal production in shallow pool habitats dominated the resource base of vertebrate predators in all habitats at the end of the summer. We could not distinguish between the trophic roles of riffle algae and terrestrial detritus, but both carbon sources appeared to play minor roles for vertebrate consumers. In shallow pools, small vertebrates, including three-spined stickleback (*Gasterosteus aculeatus*), roach (*Hesperoleucas symmetricus)*, and rough-skinned newts (*Taricha granulosa*), relied on invertebrate prey derived from local pool habitats. During the most productive summer period, growth of all size classes of steelhead and resident rainbow trout (*Oncorhynchus mykiss)* in all habitats (shallow pools, riffles, and deep unproductive pools) was largely derived from algal production in shallow pools. Preliminary data suggest that the strong role of shallow pool algae in riffle steelhead growth during summer periods was due to drift of pool invertebrates to riffles, rather than movement of riffle trout. Data for $\delta^{15}N$ showed that resident rainbow trout (25–33 cm standard length) in deep pools preyed upon small size classes of juvenile steelhead that were most often found in riffles or shallow pools. While many invertebrate consumers relied primarily on algal production derived from local habitats, our study shows that growth of top predators in the river is strongly linked to food webs in adjacent habitats. These results suggest a key role for emigration of aquatic prey in determining carbon flow to top predators.

Key words: cannibalism; carbon and nitrogen stable-isotope ratios; carbon flow; Oncorhynchus mykiss; *river food webs; scraper and collector-gatherer (SCG) taxa; spatial scale; steelhead trout; terrestrial detritus; trophic structure.*

INTRODUCTION

Food webs in adjacent habitats and ecosystems may be strongly linked by fluxes of nutrients, detritus or organisms (Polis et al. 1997). While empirical studies increasingly suggest that such linkages occur frequently (e.g., Polis and Hurd 1996, Ben-David et al. 1997, Wallace et al. 1997, Stapp et al. 1999), the spatial and temporal scales of connections between food webs remain poorly resolved. Such information is crucial to understanding processes controlling the dynamics of local populations, communities, and ecosystems, as well as the fate of fluxes of materials and individuals across habitat, ecosystem, and landscape boundaries (Polis et al. 1997, Laurance et al. 2001).

Aquatic ecologists have long recognized that trophic connections between habitats or ecosystems may strongly influence the production and structure of lake and stream food webs (Lindeman 1941, Hynes 1975, Vannote et al. 1980). The mobility of limiting nutrients, organic matter, and organisms characteristic of lotic environments suggests that such linkages are especially strong in river food webs. For example, detrital carbon inputs from terrestrial to stream food webs are important in many stream ecosystems (Hynes 1975, Vannote et al. 1980, Gregory et al. 1991, Wallace et al. 1997, Finlay 2001). However, the sources of production to river food webs at a given location are poorly known (Cooper et al. 1997, Wallace et al. 1997, Poff and Huryn 1998). Organic carbon sources for lotic food webs may be derived from multiple sources, including local

---

Manuscript received 18 December 2000; revised 8 October 2001; accepted 9 October 2001; final version received 8 December 2001.

[1] Present address: U.S. Geological Survey, 3215 Marine Street, Suite E127, Boulder, Colorado 80303 USA.
E-mail: jcfinlay@usgs.gov

[2] Present address: Stillwater Sciences, 2532 Durant Avenue, Suite 201, Berkeley, California 94704 USA.

PLATE 1. Typical riffle (foreground) and shallow pool (background) habitat in the South Fork Eel River at baseflow. Photo by J. Finlay.

algal production and the transport of particulate and dissolved organic matter from upstream habitats. These resources are patchily distributed (Pringle et al. 1988), and some invertebrate consumers are mobile. Top predators, such as fish, may be highly mobile and occupy multiple habitats within watersheds throughout their ontogeny (Schlosser 1991, 1995, Gowan and Fausch 1996). As a consequence, spatial scales of trophic interactions in rivers are largely unknown (Cooper et al. 1997). This limited resolution of the resource base of river food webs constrains our basic understanding of river ecology, as well as our ability to assess and predict human impacts.

Measurements of stable-isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are useful in understanding carbon flow and trophic structure at scales larger than those amenable to experimental or observational approaches (e.g., Schell et al. 1989, Hobson 1999). Carbon isotope ratios are effective diet tracers because there is little fractionation associated with trophic transfer of organic carbon in food webs (DeNiro and Epstein 1978, France 1996) and potential organic matter sources may have distinct $\delta^{13}C$ values (Fry and Sherr 1984, Rounick and Winterbourn 1986). Nitrogen isotope ratios indicate trophic position in food webs because of a consistent increase (+3.4‰ per trophic level for vertebrate consumers) in $\delta^{15}N$ with increasing trophic level (Minigawa and Wada 1984; but see Webb et al. [1998], Adams and Sterner [2000] for discussions of trophic fractionation by primary consumers).

The goal of this study was to understand the sources of carbon for consumers in a spatially complex lotic ecosystem. Specifically, we assessed the contribution of terrestrial detritus and epilithic algae to food webs in shallow and deep pools and riffles along a 3-km reach of the South Fork Eel River in Northern California. We used natural variation in $\delta^{13}C$ to determine carbon sources and $\delta^{15}N$ to infer trophic positions of river consumers. Analyses of $\delta^{13}C$ were particularly useful, since algal $\delta^{13}C$ varied spatially and seasonally. We then used this information to determine the spatial scales of carbon flow to food webs that support mobile top predators such as juvenile steelhead and rainbow trout.

SITE DESCRIPTION

The study was conducted in the forested headwaters of the South Fork (SF) Eel River (watershed area, 140 km^2) in Mendocino County, California, USA (39°44′ N, 123°39′ W), from spring 1997 to late summer 1999 (see Plate 1). Along the 3-km study reach, the river has a wide active channel (~30 m) with 15–40% forest canopy cover. Most precipitation falls during October–May, and discharge declines after winter rains to stable summer base flows (Fig. 1A). The river is warm and productive during the summer months, and water temperature and algal biomass peak in July (Power 1990*a, b*, 1992*a*). During this period, invertebrate assemblages are dominated by collector-gatherer and scraper functional feeding groups (Power 1992*a, b*). River habitats are composed of long, shallow pools, riffles, and deep (3–6 m) pools that have low light penetration. Filamentous green algae (*Cladophora glomerata*) are abundant in some years and sites. During this study, however, epilithic algae (i.e., films of diatoms and green algae) were dominant at the study sites. Downriver sites with high *Cladophora* abundance were not routinely sampled.

The river supports several species of anadromous salmon, but current populations are small compared to historical levels. Steelhead trout (*Oncorhynchus mykiss*), which return to the ocean after spawning, is the most abundant species. Carcasses of semelparous anadromous salmon were not observed during the 1997–1999 study period, suggesting that marine-derived organic matter inputs were not a major source of nutrients to the river. Carcasses of anadromous Pacific lamprey (*Lampetra tridentatus*) were more abundant in 1999 than the previous two years (J. C. Finlay and M. E.

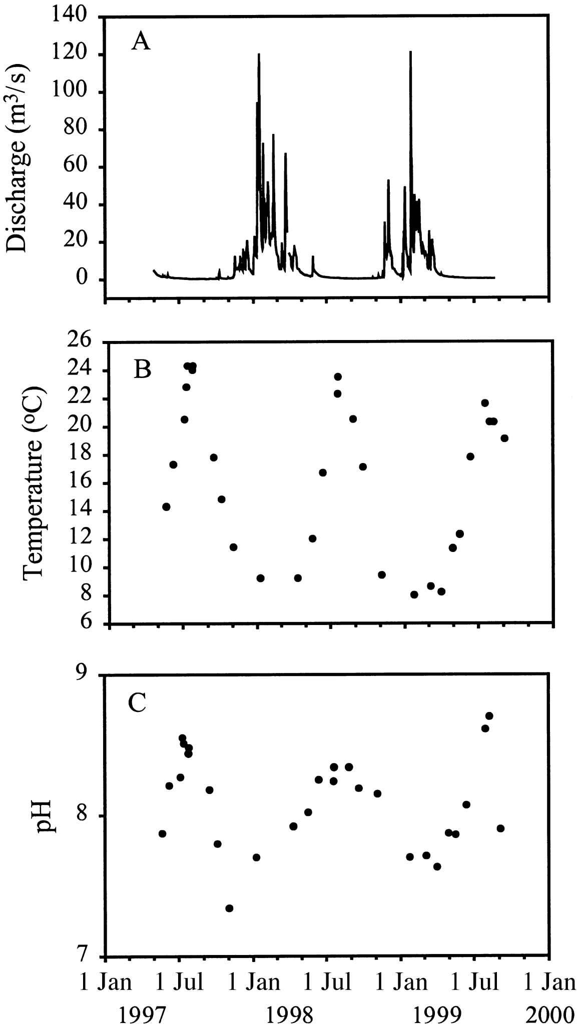

FIG. 1. (A) Discharge, (B) temperature, and (C) pH in the South Fork Eel River during 1997–1999. Discharge was measured several kilometers upstream of the study sites, and temperature and pH were measured at mid-afternoon at a single station within the study reach.

Powers, *personal observations*), and may have provided additional sources of carbon and nitrogen to the river food web.

METHODS

Physical and chemical variables

Temperature and pH were measured at least monthly (Thermo Orion, model 540A; Beverly, Massachusetts, USA) at mid-afternoon at one site in the middle of the study reaches. Discharge was calculated from stage height at a former USGS gaging station 3–6 km upstream from the study reaches. Areal extent of major habitat types in the study reach (i.e., shallow pools, deep pools, riffles) was estimated on three dates in 1998 with a meter tape.

Patterns of algal stable-isotope ratios

Spatial and seasonal variation in algal δ^{13}C was used to identify sources of production to river food webs. Environmental influences on algal δ^{13}C have been previously described for this system (Finlay et al. 1999, Finlay 2000, *in press*). Briefly, algal δ^{13}C values vary spatially in the river, because algal δ^{13}C in pools are consistently higher (by +3–12‰) than in riffles. These large between-habitat differences are consistent with the effect of water velocity on boundary layer thickness around benthic algae. Slow diffusion of CO_2 through thick boundary layers in pool habitats leads to less algal discrimination against ^{13}C, relative to riffle habitats where boundary layers are thinner and discrimination is higher. Long summer periods with stable discharge (Fig. 1A) and relatively homogenous water velocities within pool and riffle habitats produce distinct δ^{13}C of pool vs. riffle algae.

Seasonal changes in algal δ^{13}C within a given habitat (i.e., pools or riffles) are characterized by higher values during summer and fall base flow periods than winter or spring. These patterns are caused by increased δ^{13}C of dissolved inorganic carbon and decreased algal discrimination against ^{13}C during productive base flow periods.

Algal δ^{15}N values also vary temporally within the South Fork Eel River, but much less is known about the controlling mechanisms. Algal δ^{15}N values show an opposite seasonal pattern to δ^{13}C, possibly due to changes in δ^{15}N of dissolved inorganic nitrogen, or discrimination against ^{15}N by algae (Wada and Hattori 1978, Cifuentes et al. 1989).

Stable-isotope ratios of algae, detritus, and macroinvertebrates

Epilithic algae and larval stages of common invertebrates were sampled at two to five adjacent shallow pool–riffle pairs for each sampling period. Deep pools ($>$3 m depth) were not sampled, because we assumed low production in these habitats due to low light penetration and sandy substrata.

Samples of epilithic algae were collected from cobbles with a wire or nylon brush, filtered and dried. Microscopic examination of epilithic algal samples collected in this manner showed that most matter was composed of an assemblage of diatoms (*Achnanthes minutissima*, *Cocconeis* spp., and *Epithemia* spp.) and, to a lesser extent, filamentous green algae (*Cladophora glomerata*). Cyanobacteria (*Nostoc pruniforme*) were avoided because of inedibility to most invertebrates at the study site (Dodds et al. 1995).

Sampling of algae and invertebrates was conducted in two ways. First, samples for epilithic algae (several samples per site, each sample a composite of two or three subsamples) and invertebrates (samples of 2–40 individuals composited from three to seven cobbles for each taxon within the habitat) were collected to characterize algal and invertebrate functional feeding group stable-isotope ratios by habitat (i.e., shallow pools and riffles). Scraper and collector-gatherer taxa were considered as a single group (hereafter ''SCG''), because there were no differences in stable-isotope ratios between groups (Finlay 2000). Shallow pools and riffles were defined as habitats with laminar and turbulent flow, respectively. Samples from extremely slow-flow (i.e., shallow near-shore habitats with water velocity <0.03 m/s) and fast-flow (i.e., top surfaces of rocks in fast riffle flows) environments were not included, because such habitats composed a very low percentage of the total area of the riverbed.

Second, epilithic algae and invertebrates were sampled along continuous gradients of water velocity. Since algal $\delta^{13}C$ are strongly influenced by water velocity (Finlay et al. 1999), this sampling method allowed us to assess the foraging range of invertebrate consumers at a finer scale than the first method. Each sample was collected by compositing algae, SCG, or invertebrate predators (2–40 larvae for each invertebrate species or taxon) from one or two adjacent cobbles with similar water velocity. Water velocity was measured ~6 cm above the sampled substrata with a Marsh McBirney flow meter (Model 2000; Marsh McBirney, Frederick, Maryland, USA). To characterize algal and invertebrate stable-isotope ratios by habitat, as described for the first sampling method, data were averaged by group for each habitat. As above, data from extremely slow and fast flow environments were not included in these averages.

Scrapers and collector-gatherer taxa were primarily Ephemeroptera (*Timpanoga* sp., *Nixe* sp., *Epeorus* sp., *Baetis* spp.) and Trichoptera (*Dicosmoecos gilvipes*, *Gumaga* sp., *Neophylax* spp., *Glossosoma* sp., *Psychoglypha* sp.) larvae. Filter feeders were Simuliidae and Hydropsychidae (*Hydropsyche* spp.), and invertebrate predators were primarily Plecoptera (*Calineuria californica*, *Hesperoperla* sp.), Hemiptera (*Ambrysus mormon*), and Odonata (*Aeshna californica*, *Ophiogomphus* sp.). Trichopteran shredders were not routinely sampled because of their low abundance. For most invertebrate samples, gut contents were removed within several hours of collection by dissection and were discarded. When dissection was not possible (i.e., for small taxa), larvae were held for 24 h without food, for gut clearance, before rinsing and drying. Samples were dried at 50°C for ~48 h.

We used the strong relationship between algal and SCG $\delta^{13}C$ in shallow pools and riffles (Finlay et al. 1999) to infer algal $\delta^{13}C$ when direct measurements were not made. This relationship was further evaluated with additional sampling of algal and SCG $\delta^{13}C$. Samples for SCG $\delta^{13}C$ were easier to collect and analyze than epilithic algal $\delta^{13}C$. Algal $\delta^{15}N$ was not measured routinely, due to difficulties obtaining enough biomass for $\delta^{15}N$ analyses.

Samples for stable carbon isotope ratios of suspended particulate organic matter (SPOM) were collected by filtering 0.7–1.5 L of river water onto a pre-ashed glass fiber filter (Whatman GF/F, nominal pore size 0.7 μm; Whatman, Clifton, New Jersey, USA). Samples of terrestrial detritus were collected for stable isotope analyses from patchy deposits (area, 0.2–1 m^2) of coarse benthic organic matter (CBOM) in pools. Subsamples from CBOM deposits were sorted into leaves, fine benthic organic matter (FBOM, particles <1 mm), and woody material, and were dried at 50°C to a constant mass. Samples of leaves and FBOM were ground in a Wiley mill and mortar and pestle, respectively, before stable isotope analysis. In midsummer 1997 and 1998, shredders (usually 5–10 *Lepidostoma* sp.) were collected from CBOM and adjacent cobbles with epilithic algae in shallow pool habitats. Samples of shredders were processed and analyzed as we have described.

Draft sampling

To measure invertebrate dispersal and stable-isotope ratios (three periods during summer 1998), we placed drift nets at the end of shallow pools or riffles after dusk or at midday. Two quantitative samples were collected after 10–20 min, depending on flow, in 363-μm mesh nets. Samples were preserved in 70% ethanol until processing. Stable isotope samples were collected after ~30 min in one or two other nets, and sorted later that evening. After sorting, isotope samples were processed as for benthic invertebrate stable isotope samples.

Stable-isotope ratios of vertebrates

Roach (*Hesperoleucas symmetricus*), stickleback (*Gasterosteus aculeatus*), and rough-skinned newts (*Taricha granulosa*) were collected with dip nets or minnow traps from shallow pool habitats. Small fishes were euthanized and frozen shortly after collection; several large roach were fin clipped. For small fishes, stable-isotope analyses were done on acid-treated, dried, and ground whole individuals after dissection and removal of gut contents. For larger roach collected whole, dorsal muscle samples were dissected and dried. For newts, samples for stable-isotope analyses were collected by toe clipping individuals. Toe clip samples from newts were acid treated prior to grinding and analysis.

We used nondestructive samples of fin tissues, rather than standard muscle tissue, samples to measure stable-isotope ratios of steelhead and resident rainbow trout and large roach, because we expected no differences between stable-isotope ratios of fins and muscle (Rounick and Hicks 1985). To establish the relationship between fin and muscle tissues, we analyzed muscle tissue stable-isotope ratios from trout that were killed as a result of incidental mortality or from two trout that were found freshly dead. Trout were collected along a 3-km length of the river by angling from adjacent shallow pools and riffles in early June and late August 1998, and from deep pools in late August. For both sampling periods, epilithic algae was the dominant growth form at most sites, although in late August several shallow-pool sites had 10–35% cover of *Cladophora*. Masses and lengths of trout were measured (standard length, SL), and small sections of caudal or anal fins were clipped from each fish (see Tyus et al. 1999).

Young-of-the-year trout (1–5 cm SL) were not routinely sampled in the spring, because maternal nitrogen and carbon of marine origin obscured trophic position and diet information. Elevated young-of-the-year trout $\delta^{15}N$ (between +12–17‰ depending on size; J. C. Finlay, *unpublished data*) were similar to adult Pacific salmon $\delta^{15}N$ reported by Bilby et al. (1996). The marine isotopic signature of maternal steelhead persisted in young trout until individuals were >5 cm standard length (SL).

Stable-isotope analyses

Dried epilithic algae, invertebrates, and vertebrate predator tissues were ground to a powder before stable carbon and nitrogen isotope analyses on a Europa 20-20 continuous flow isotope ratio mass spectrometer (PDZ Europa, Cheshire, UK). Lipids were not extracted from invertebrate samples (see Finlay et al. 1999) or fish samples, because we expected little variation in lipid content of fin tissues. Values of $\delta^{13}C$ are expressed relative to the Pee Dee Belemnite (PDB) standard, and values of $\delta^{15}N$ are expressed relative to the atmospheric nitrogen standard. Approximately 20% of samples were analyzed in duplicate, and the mean standard deviations were usually <0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ analyses. Means for epilithic algae, SCG, black flies, hydropsychid caddisflies, and predators in pool and riffle habitats were calculated by averaging data for all taxa within each group.

Carbon isotope mixing model

Provided that sufficient isotopic variation between organic matter sources exists, mixing models may be used to estimate contributions of potential food sources to consumers (Fry and Sherr 1984, Phillips and Gregg 2001). Riffle and pool algal $\delta^{13}C$ were distinct for base flow periods, including those following food web sampling in early June 1998, until the sampling of trout stable-isotope ratios in late August. We used these differences in a two-source mixing model to calculate contributions of shallow-pool and riffle algal carbon to diets of steelhead and rainbow trout at the end of the summer growing season of 1998. There were no within-habitat differences for $\delta^{13}C$ between algae and scraper and collector-gatherer (SCG) taxa (*t* tests, $P > 0.05$), so we used means of all algae and SCG $\delta^{13}C$ values for July in shallow pools ($-18.9 \pm 0.5‰$) and riffles ($-23.6 \pm 0.5‰$) for end members in the model. We assumed no contribution of terrestrial detritus-based food webs to fish diets (see Results and Discussion). Mean and error estimates were made according to equations from Phillips and Gregg (2001). Fish $\delta^{13}C$ were corrected for trophic enrichment of +0.5‰ per trophic level. This value is less than the +1‰ increase per trophic level often assumed in marine food webs, and is used because of the observation of low trophic fractionation of carbon by freshwater consumers (France 1996). Trophic position was estimated from consumer $\delta^{15}N$ (see Vander Zanden and Rasmussen 1999).

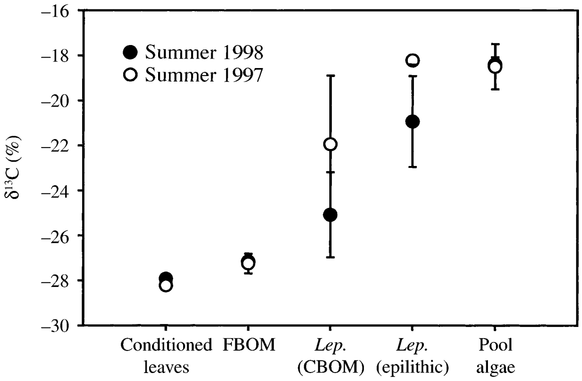

FIG. 2. Mean stable carbon isotope ratios (means ± 1 SE) for the shredder *Lepidostoma* sp. (*Lep.*) and potential organic carbon sources. Data for conditioned leaves and fine benthic organic matter (FBOM) are means from material sorted from deposits of coarse benthic organic matter (CBOM) in 1997 and 1998. We sampled 5–10 *Lepidostoma* from CBOM deposits or epilithic surfaces in areas of pools with water velocities of 0.03–0.05 m/s. Data for pool algae are means for epilithic algae during each sampling period.

RESULTS

Physical and chemical variables

Temperature and pH increased during summer base flow to mid-July maxima in all years (Fig. 1). Dissolved CO_2 (*aq*) was lower than atmospheric levels during July and August (Finlay 2000), suggesting peak algal demand for carbon during these months.

Shallow pools were the dominant habitat in terms of surface area within the 3-km study reach in early June (50%) and late August (70%). Riffle area decreased from 26% in June to 14% by late August. Deep pool area decreased from 24% in June to 16% in late August.

Terrestrial-detritus stable-isotope ratios

Stable carbon isotope ratios of terrestrial detritus (river-conditioned leaves and fine benthic organic matter [FBOM] from deposits of coarse benthic organic matter [CBOM]) sampled from shallow pools in summer 1997 and 1998 (Fig. 2) were similar to typical values for terrestrial C_3 plants (i.e., −28‰). We did not measure terrestrial detritus $\delta^{13}C$ at other times of the year in the South Fork Eel River, but variation in stream-conditioned leaves and shredders in two nearby tributary streams was low (all values within 2‰) over eight sampling dates during spring, summer, and fall periods (J. C. Finlay, *unpublished data*).

Algal and benthic invertebrate stable-isotope ratios

Stable carbon isotope ratios of benthic invertebrates indicated strong reliance on algal carbon by some functional feeding groups (scrapers, collector-gatherers, and predators) and at least partial reliance on algal resources by others. At the habitat scale (i.e., within shallow pools or riffles) and in smaller patches (one to two adjacent cobbles), δ^{13}C from scraper and collector-gatherer (SCG) taxa were strongly related to epilithic algal δ^{13}C, suggesting reliance on local sources of algal production by the dominant functional feeding groups (i.e., scrapers and collector-gatherers) in the river. At the habitat scale, SCG δ^{13}C tracked variation in algal δ^{13}C in shallow pool and riffle habitats for the months June–October during 1997–1999. Mean SCG δ^{13}C values were strongly related to mean epilithic algal δ^{13}C in both habitats (linear regression relationship: SCG δ^{13}C = 0.88(algae) – 2.84, $P > 0.001$, $r^2 = 0.97$). On average, epilithic algal δ^{13}C were slightly ^{13}C-enriched (mean ± 1 SE, +0.33‰ ± 0.23) relative to SCG δ^{13}C.

In mid-July 1999, SCG δ^{13}C closely tracked small-scale variation in algal δ^{13}C (Fig. 3A) related to water velocity effects on boundary layer thickness around benthic algal cells (Finlay et al. 1999). Similar relationships between SCG δ^{13}C and water velocity were observed on other dates during base flow periods of 1998 and 1999 (Fig. 3B). Since these samples were collected by compositing algae (July 1999 only) and SCG (three dates) from small habitat patches (i.e., adjacent cobbles with similar water velocity), our results indicate that SCG largely relied on local sources of algal production, consistent with limited mobility of benthic grazers. For the July 1999 results, algal δ^{13}C were slightly ^{13}C-enriched, on average, relative to SCG δ^{13}C (Fig. 3A).

Riffle algae and SCG δ^{13}C were consistently lower than in shallow pools, and the differences between habitats increased during the summer base flow period (Fig. 4A) when pH was highest (Fig. 1C) and CO_2 (*aq*) was lowest (Finlay 2000). We used these consistent habitat differences in algal and SCG δ^{13}C as a natural tracer of algal production derived from each habitat through river food webs, during summer base flow periods.

Algal and SCG δ^{13}C within shallow pools and riffles were also seasonally variable, providing a tracer of algal contributions to river food webs during spring vs. summer. In both habitats, SCG δ^{13}C increased from spring to summer, while δ^{15}N decreased (Fig. 4A, D).

Stable-isotope ratios of filter feeders (black flies and hydropsychid caddisfly larvae) in riffles, and invertebrate predators in shallow pools and riffles, followed the seasonal patterns of algae and SCG (Fig. 4), suggesting at least partial reliance on algal carbon. For filter feeders, δ^{13}C values were usually intermediate between riffle and pool algal δ^{13}C, but approached pool algal δ^{13}C values during midsummer (Fig. 4B). Values of δ^{13}C in suspended particulate organic matter (SPOM; −28‰ to −26‰) were similar to values for terrestrial detritus (−28‰). During midsummer, SPOM values were ^{13}C-depleted relative to black fly and hydropsychid δ^{13}C (Fig. 4B), indicating selective feeding on or assimilation of algae in the water column derived from shallow pools by filter feeding invertebrates. Hydropsychid δ^{15}N were usually higher than black fly δ^{15}N, consistent with predation on drifting invertebrates as well as consumption of particulate organic matter.

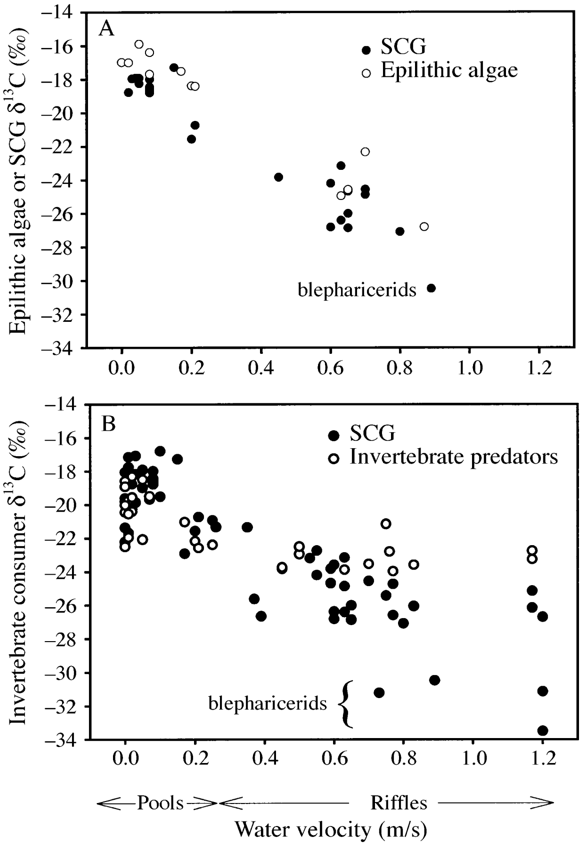

FIG. 3. The relationships of (A) δ^{13}C from epilithic algae and scraper and collector-gatherer (SCG) taxa to water velocity during mid-July 1999, and (B) δ^{13}C from SCG and invertebrate predators to water velocity during base flow periods in 1998 and 1999. For SCG, taxa sampled were primarily Ephemeroptera and Trichoptera, except in fast water velocities where data for blephariceríd larvae were also included. Unlike other riffle herbivores, blephariceríds graze on rock tops in fast flowing water. (A) Each point represents a composited sample of epilithic algae or SCG within a 1-m^2 patch with similar water velocity within a pool or riffle. The slope of relationships with water velocity for algae ($y = -11.48x - 16.13$, $r^2 = 0.93$) and SCG ($y = -12.39x - 17.56$, $r^2 = 0.91$) was highly significant in both cases ($P < 0.001$), and the regression slopes were not significantly different from each other (t tests, $P > 0.05$). However, the intercept value was significantly greater (t tests, $P < 0.05$) for the algae–water velocity relationship than for the SCG–water velocity relationship. (B) Data for blephariceríd larvae for two dates in midsummer 1997 were used to supplement SCG data from 1998–1999.

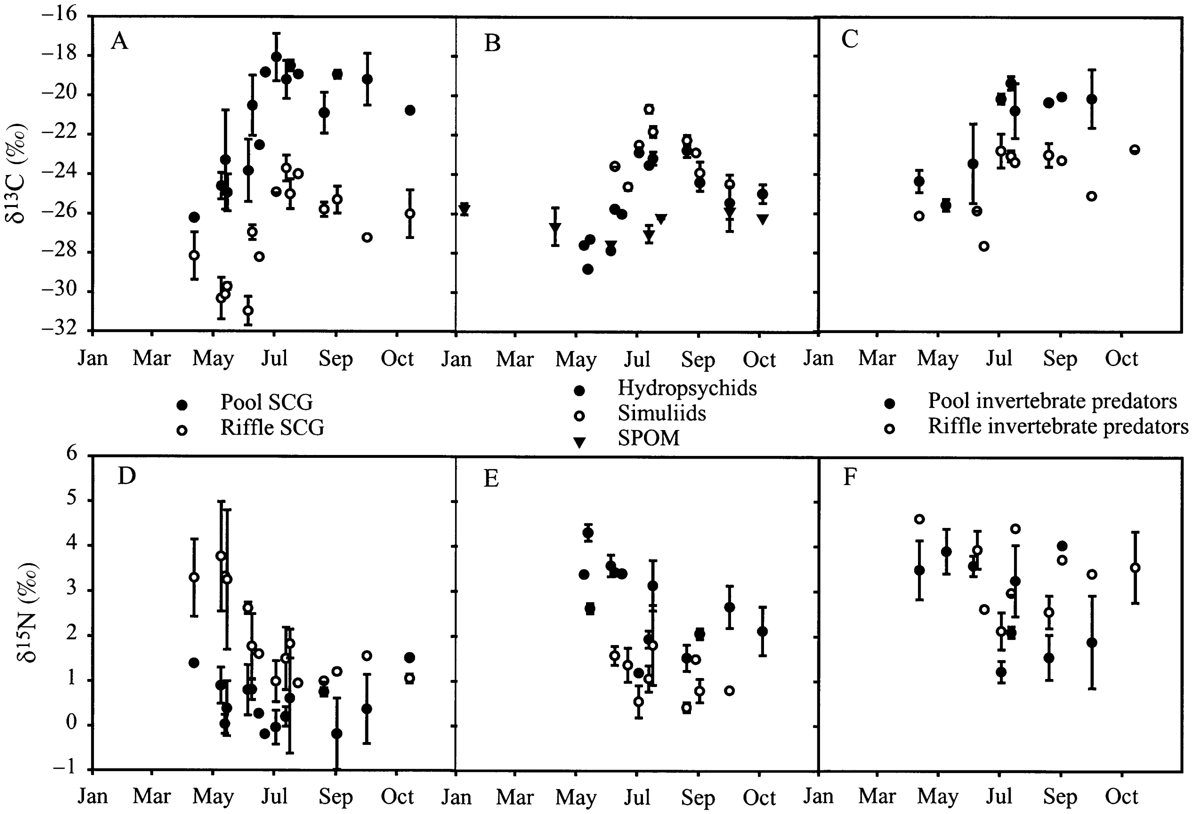

FIG. 4. Seasonal patterns in $\delta^{13}C$ and $\delta^{15}N$ of (A and D) scraper and collector-gatherer (SCG) taxa in riffles and shallow pools, (B and E) filter feeders and suspended particulate organic matter (SPOM), and (C and F) invertebrate predators. Each key pertains to the panels situated directly above and directly below the key. Data are from 1997–1999, and error bars are means ± 1 SE.

Invertebrate predator $\delta^{13}C$ tracked variation in algal and SCG $\delta^{13}C$ in shallow pools but not riffles (Fig. 5). On average, riffle predator $\delta^{13}C$ were ^{13}C-enriched relative to riffle SCG $\delta^{13}C$ by 2‰ (−25.1 ± 0.2‰ for SCG vs. −23.1 ± 0.2‰ for predators for all base flow data; Fig. 3B), indicating partial reliance on shallow-pool-derived algal carbon, through either consumption of invertebrates dispersing from pools or filter feeders.

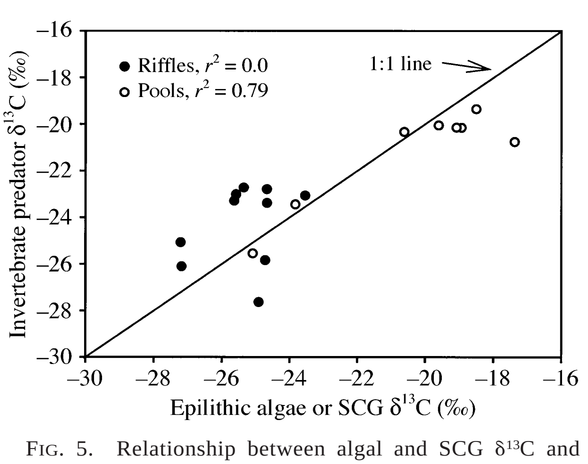

FIG. 5. Relationship between algal and SCG $\delta^{13}C$ and invertebrate predator $\delta^{13}C$ in pools and riffles. The relationship was significant in pools ($P = 0.002$, $r^2 = 0.79$, $n = 8$), but not in riffles ($P = 0.38$, $r^2 = 0.0$, $n = 10$).

Differences in between $\delta^{15}N$ of invertebrate predators and SCG were less than the expected 3.4‰ increase between predators and prey. During base flow periods, mean invertebrate predator $\delta^{15}N$ values were 1.5‰ greater than SCG $\delta^{15}N$ (mean ± 1 SE, 2.5 ± 0.2, compared to 1.0 ± 0.2, respectively; data not shown). Water velocity explained very little variation in invertebrate predator or SCG $\delta^{15}N$ during base flow conditions ($r^2 = 0.00$ and 0.07, respectively; data not shown).

Stable-isotope ratios of shredders (primarily *Lepidostoma* sp.) collected from deposits of CBOM in shallow pools were ^{13}C-enriched relative to conditioned leaves indicating partial reliance on epilithic algae during 1997 and, to a lesser extent, 1998 (Fig. 2). *Lepidostoma* $\delta^{13}C$ for individuals sampled from adjacent epilithic habitats were more similar to epilithic algal $\delta^{13}C$ than leaves demonstrating partial (1998) or complete (1997) reliance on algal carbon by shredders (Fig. 2).

Drifting invertebrates

Stable carbon isotope ratios of drifting baetid mayflies suggested that dispersing collector-gatherers relied

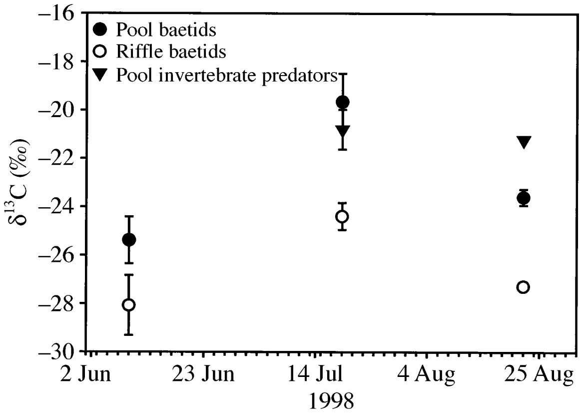

FIG. 6. Stable-carbon isotope data for drifting pool and riffle baetid mayflies in 1998. Some pool baetids were collected in riffle samples and had δ^{13}C similar to pool baetids drifting from pools. Data for predators drifting from pools into riffles are also included. Error bars indicate ±1 SE.

on algal production within the habitat they had departed. During three dates in 1998, baetid mayflies drifting from shallow pools and riffle habitats had similar δ^{13}C to algae and SCG in shallow pools and riffles, respectively (Figs. 4A and 6).

Vertebrates

Roach, three-spined stickleback, and newt δ^{13}C values in shallow pools were similar to algal and SCG δ^{13}C within these habitats, indicating strong reliance on food webs supported by shallow pool algae (Fig. 7). Stable carbon isotope ratios of drifting invertebrates indicated that invertebrate prey sources for small vertebrates were of local origin in shallow pools, and not mediated through prey immigration from upstream habitats into shallow pools. Baetid mayflies drifting from riffles to shallow pools had δ^{13}C values consistent with riffle carbon sources, and riffle carbon appeared to play a minor role, if any, for small vertebrates (Fig. 7).

Stable-isotope ratios of trout fin and muscle tissue were similar, so data for fin isotope ratios were used to infer muscle data. In 1998, fin data closely matched muscle (m) data for δ^{13}C (fin = $0.99m + 0.22$, $r^2 = 0.99$) and δ^{15}N (fin = $1.04m - 0.26$, $r^2 = 0.97$). In 1999, however, slopes for similar relationships for both δ^{13}C and δ^{15}N were significantly different from 1 (J. C. Finlay, *unpublished data*) suggesting that such relationships must be assessed annually.

Trout stable-isotope ratios varied seasonally, but were consistent with summer growth of trout in all habitats that was largely derived from algal production in shallow pools. For individuals 10–15 cm SL, trout δ^{13}C increased from early June–late August by 4–6‰, and δ^{15}N decreased by 2–3‰ (Fig. 8B, D). Low trout δ^{13}C and high δ^{15}N in June are consistent with some trout growth during spring, because SCG δ^{13}C and δ^{15}N were, respectively, lower and higher during April and May than summer and fall (Fig. 8). By late August, however, trout δ^{13}C for all size classes and habitats were

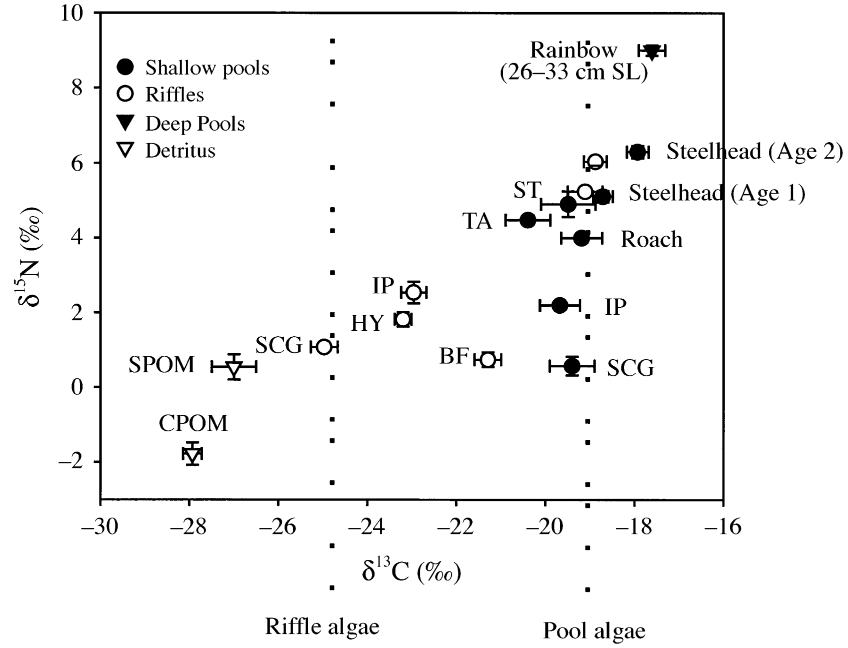

FIG. 7. Dual isotope plot of detritus and consumer δ^{13}C and δ^{15}N in July and August 1998 for the three main habitats in the river. Values for algae and invertebrate consumers represent mean values (±1 SE) for all samples in July and August; values for vertebrates are from samples collected in mid-August. Dotted vertical lines represent mean algal δ^{13}C in pool and riffle habitats. Abbreviations are: H, invertebrate SCG; HY, hydropsychid caddisflies; BF, black flies; IP, invertebrate predators; ST, three-spined stickleback; and TA, *Taricha granulosa*.

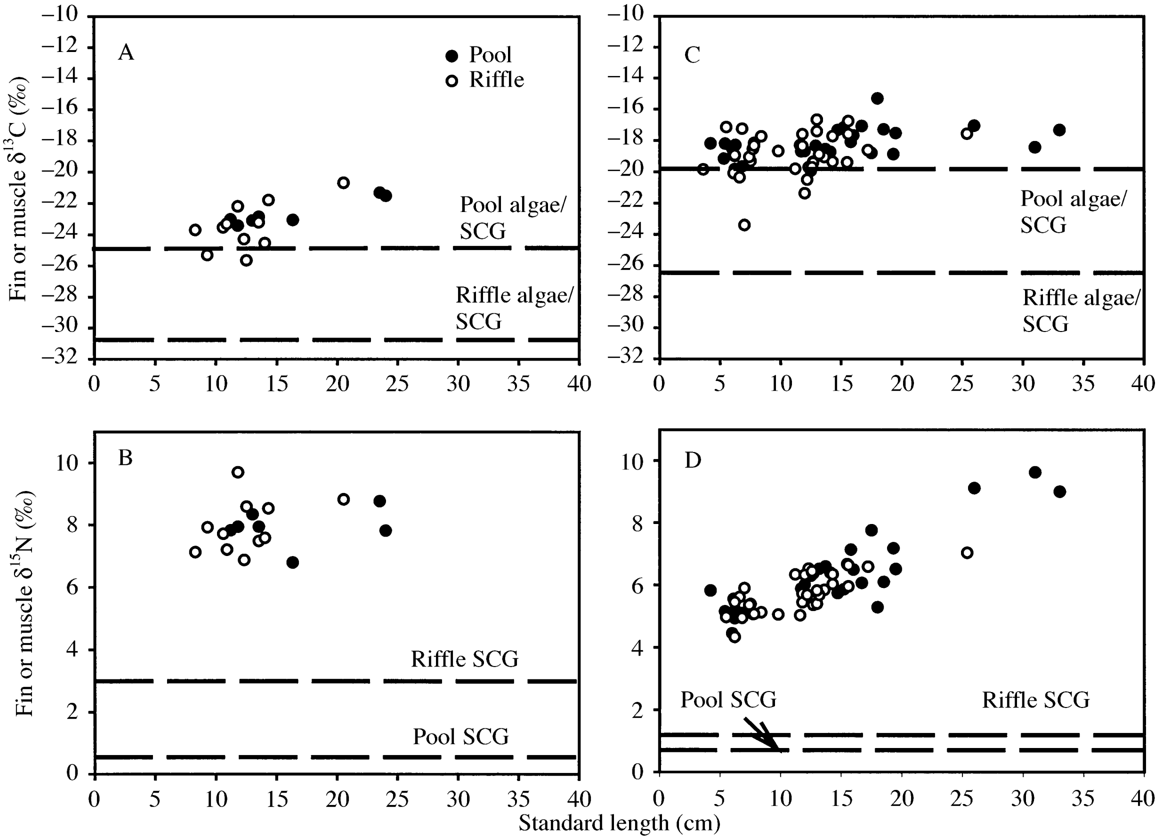

FIG. 8. Steelhead trout standard length (SL) vs. (A) δ^{13}C and (B) δ^{15}N in June 1998, and vs. (C) δ^{13}C and (D) δ^{15}N in late August 1998. (A) and (C): Dashed lines represent mean algae and scraper and collector-gatherer (SCG) δ^{13}C in pools and riffles. (B) and (D): Dashed lines represent mean SCG δ^{15}N in pools and riffles. In June, trout δ^{13}C increased with SL in pools ($P = 0.001$, $r^2 = 0.88$) and riffles ($P = 0.043$, $r^2 = 0.31$). Trout δ^{15}N were unrelated to SL in both pools ($P = 0.64$, $r^2 = 0.0$) and riffles ($P = 0.22$, $r^2 = 0.07$). In August, trout δ^{13}C increased slightly with SL in pools ($P = 0.033$, $r^2 = 0.15$), but not in riffles ($P = 0.15$, $r^2 = 0.03$). Trout δ^{15}N increased with SL in both pools ($P < 0.001$, $r^2 = 0.64$) and riffles ($P < 0.001$, $r^2 = 0.44$).

TABLE 1. Results of two-source mixing model to calculate contributions of algal production in shallow pools and riffles to diets of steelhead and rainbow trout.

Habitat	Standard length (cm)	n	Percentage pool algae (mean ± 1 SE)	Percentage riffle algae (mean ± 1 SE)
Riffle	3.6–9.8	14	68.8 ± 9.2	31.2 ± 9.2
Riffle	11.2–19.9	22	73.7 ± 9.0	26.3 ± 9.0
Shallow pool	4.2–7.8	7	77.2 ± 9.3	22.8 ± 9.3
Shallow pool	11.7–19.9	16	93.8 ± 10.7	6.2 ± 10.7
Deep pool	26–33	4	90.1 ± 13.7	9.9 ± 13.7

Notes: Results presented here are based on primary consumer δ^{15}N values and an expected increase of 3.4‰ per trophic level (Vander Zanden and Rasmussen 1999). We assume that juvenile steelhead trout (<10 cm SL) had a trophic position of 3.3, that juvenile steelhead trout (10–20 cm SL) had a trophic position of 3.7, and that larger trout (28–32 cm SL) had a trophic position of 4.5. Small differences between scraper and collector-gatherer taxa and invertebrate predators δ^{15}N (i.e., ~1.5‰) leave some uncertainty as to the true trophic position of top predators. While the correspondence of trophic fractionation of δ^{15}N and trophic position in food webs has been well tested for freshwater fish (Vander Zanden et al. 1997), less is known about trophic fractionation of invertebrate consumers.

very similar to mean algal and invertebrate δ^{13}C in shallow pools (Fig. 7). There were no differences in trout δ^{13}C between sites dominated by epilithic algal and those where *Cladophora* was present (J. C. Finlay, *unpublished data*).

Using a stable-carbon isotope mixing model, we inferred that trout growth in all habitats was highly dependent on algal production in shallow pools by the end of summer (Table 1). Although riffle trout did rely in part on riffle algal production, there was no relationship between mean riffle trout δ^{13}C and riffle size (i.e., area) for late August data ($P = 0.24$, $r^2 = 0.08$, $n = 9$; data not shown).

Trout δ^{15}N increased with length (Fig. 8D), showing increasing trophic position with size during summer base flow periods. Large rainbow trout (25–32 cm SL) in deep pools had δ^{15}N values ~4‰ higher than the smallest size classes of steelhead trout sampled from riffles or shallow pools (Figs. 7 and 8D). Assuming a 3.4‰ increase in δ^{15}N per trophic level above primary consumers (Vander Zanden et al. 1997), these data suggest predation on smaller size classes of juvenile steelhead by large trout and predation on roach by intermediate size classes of juvenile steelhead. Gut content observations for larger trout almost always revealed the presence of smaller steelhead or other vertebrates (J. C. Finlay, *unpublished data*).

DISCUSSION

Algal and terrestrial carbon sources for river consumers

The River Continuum Concept (Vannote et al. 1980) predicts the increased importance of algal relative to terrestrial carbon sources to consumers in mid-order river reaches such as the South Fork (SF) Eel River. However, the relative contribution of these sources to primary consumers and predators has not been quantified in most previously studied river food webs (but see Doucett et al. [1996]). We used seasonal and spatial variation in algal $\delta^{13}C$ to examine the contributions of algal and terrestrial carbon sources to river consumers. Our results suggest that the carbon base of shallow pool and riffle food webs is dominated by algal production, and that terrestrial detritus plays a minor role as a carbon source for top predators in all habitats.

The strong relationship observed between algal $\delta^{13}C$ and $\delta^{13}C$ from scraper and collector-gatherer (SCG) taxa in pool and riffle habitats and along water velocity gradients (Fig. 3A) suggests that the numerically dominant invertebrate consumer groups (i.e., SCG; Power 1992*b*) relied primarily on algal carbon sources. However, on average, SCG $\delta^{13}C$ were slightly ^{13}C-depleted (-0.33‰) compared to epilithic algae in pool and riffle habitats. Scraper and collector-gatherer $\delta^{13}C$ values were similarly ^{13}C-depleted relative to algae for mid-July samples along a water velocity gradient (Fig. 3A). The lower SCG $\delta^{13}C$ compared to algae within a given habitat is inconsistent with expected trophic enrichment of herbivores (0 to $+1$‰) relative to algae. However, the absence of herbivore ^{13}C enrichment relative to plants has been observed elsewhere (Vander Zanden and Rasmussen 2001).

In the SF Eel River, we suggest two alternative explanations for the lack of increase in herbivore $\delta^{13}C$ relative to their algal resources. First, SCG may have consumed a surface layer of epilithic algae that was ^{13}C-depleted relative to the sampled epilithic matrix. Such depletion could arise from greater access to CO_2 (*aq*), and thus increased discrimination against $^{13}CO_2$, by the surface layer of algae compared to underlying algal cells (Calder and Parker 1973, Pardue et al. 1976). The surface layer of algae is most available to invertebrate herbivores.

Second, SCG $\delta^{13}C$ may have been influenced by consumption of a small amount of ^{13}C-depleted carbon, such as terrestrial detritus. While epilithic films are strongly dominated by algae and dissolved organic carbon (DOC) concentrations are low in the SF Eel River, a small amount of assimilation of terrestrial carbon could account for the observed ^{13}C-depletion of SCG relative to algae. However, if consumption of terrestrial detritus (-28‰) did contribute slightly to consumer diets for the July 1999 data (Fig. 3A), the regression slope of the relationship between water velocity and SCG $\delta^{13}C$ should be lower than for the relationship between water velocity and algal $\delta^{13}C$. In contrast, the slope of the water velocity–algae relationship was lower than for the water velocity–SCG relationship, suggesting that consumption of terrestrial carbon might not account for the algal ^{13}C-enrichment relative to SCG in mid-July.

Other primary consumers relied at least in part on algal carbon. Shredders, expected to primarily consume coarse terrestrial leaf detritus, relied on both epilithic algal and terrestrial carbon (Fig. 2). Shredders (i.e., *Lepidostoma* sp.) relied more heavily on terrestrial carbon in deposits of terrestrial detritus than in epilithic substrata in shallow pools, but such deposits cover only a small percentage ($<3\%$) of the river bottom (Finlay et al. 1999). On epilithic substrata, shredders compose a small percentage of invertebrate biomass (Power 1992*b*).

Midsummer $\delta^{13}C$ of filter feeders (simuliids and hydropsychids) were intermediate between shallow pool algal $\delta^{13}C$ and riffle algal or terrestrial detritus $\delta^{13}C$, suggesting substantial use of algal carbon from shallow pools (Fig. 4B). Because riffle algal and terrestrial detritus $\delta^{13}C$ were often similar, we could not assess the contribution of riffle algae or terrestrial detritus in providing the balance of filter feeder diets.

Our two-source mixing model results demonstrated a large contribution of algal carbon to the growth of top predators in the river. These analyses showed that the diets of trout in all three major habitats in the river are dominated by algal production in shallow pools during summer base flows (Table 1).

The mixing model results may be sensitive to several of our assumptions. First, we assumed no contribution of terrestrial detritus to fish diets, because variation in scraper and collector-gatherer $\delta^{13}C$ was explained by algal $\delta^{13}C$. However, if terrestrial detritus $\delta^{13}C$ (-28‰ for coarse benthic organic matter [CBOM] in 1998) was used as a mixing model endpoint instead of riffle algae $\delta^{13}C$, estimated contributions of pool algae to trout diets would be ~20% higher than for the riffle algal $\delta^{13}C$ endpoint, and terrestrial detritus would account for a very low percentage of trout diets (minimum, 7.2%; maximum 19.5%; depending on habitat). Although we cannot resolve the contribution of riffle algae vs. terrestrial detritus to trout with $\delta^{13}C$ data alone, our results demonstrate the contribution of either source to trout is small relative to that of pool algae.

Second, we used algal and SCG $\delta^{13}C$ from the period of peak productivity (i.e., mid-July) as source end points for the model. Algal $\delta^{13}C$ were slightly lower in mid-August in both shallow pools (mean ± 1 SD, -19.5 ± 1.3‰; $n = 5$) and riffles (-26.1 ± 2.3‰, $n = 5$).

Use of these end points in the mixing model would yield substantially higher estimates (minimum 88%, maximum 100%) of pool algal contributions to trout diets compared to use of the mid-July end points.

Finally, we assumed that trout were in isotopic equilibrium with their prey when trout were sampled in August. We made this assumption because growth of juvenile trout should be rapid during the warm and productive summer months (Fig. 1B, C). Furthermore, we would expect large differences in $\delta^{13}C$ related to fish size if trout were not in isotopic equilibrium with their prey because of differences in tissue turnover times between small and large trout (Hesslein et al. 1993). Since such differences were not observed (Fig. 8C), our last assumption seems reasonable. However, if trout $\delta^{13}C$ were not at equilibrium with summer prey $\delta^{13}C$ (that is, increasing from ^{13}C-depleted June values), then trout $\delta^{13}C$ at equilibrium would be higher than the values used in the model. The use of higher trout $\delta^{13}C$ values would yield greater calculated contributions of pool algae to trout diets than estimated in Table 1. Thus, based on these three evaluations of critical assumptions involved in our calculations, we suggest that the mixing model estimates are conservative with respect to the contribution of shallow pool algae to trout diets.

General understanding of the controls of algal vs. terrestrial contributions to river food webs is incomplete (Wallace et al. 1997, Finlay 2001). In the SF Eel River, the observed limited importance of terrestrial carbon is at least in part due to the high algal biomass observed during summer base flows (Power 1990*a, b,* 1992*a*). However, limited supply or low quality of terrestrial detritus could also reduce its use by river consumers. For example, the wide active channel of the river, maintained by winter flooding, may limit inputs of fresh litterfall by preventing tall terrestrial vegetation from establishing near the water's edge during summer base flow. Furthermore, dissolved organic carbon (DOC) concentrations are low (1–2 mg/L) in tributary streams in the watershed. Low DOC may be the result of rainless summers, retention of DOC in soils, or the absence of wetlands in the watershed. Export of particulate organic carbon from tributary streams to the SF Eel River may also be reduced by the absence of summer rainfall (Fig. 1A), as observed elsewhere (Golladay 1997). Finally, the poor nutritional quality of plants in old-growth conifer forests (e.g., Wipfli 1997), such as those found in the Eel River watershed, could limit the rate of transfer of organic carbon from forest detritus to river food webs.

Spatial scale carbon flow to river consumers

The productivity and structure of river food webs are highly influenced by processes occurring in adjacent or upstream ecosystems (Vannote et al. 1980, Wallace et al. 1997), but the nature and strength of connections between habitats remain largely unknown. We suggest two main reasons for this. First, while stream and river ecosystem metabolism and organic matter budgets are extensively described, the sources of organic carbon for river consumers are difficult to assess. Several recent studies have clearly shown that large standing stocks or fluxes of terrestrial organic carbon might not necessarily provide the primary carbon sources for river consumers (e.g., Araujo-Lima et al. 1986, Mayer and Likens 1987, Hamilton et al. 1992, Peterson et al. 1993). Second, experimental approaches are often confined to spatial scales too small to discern the importance of multiple potential sources of production supporting mobile and long-lived consumers such as fish. Stable-isotope tracers of organic matter may link previous approaches to understanding carbon flow in river food webs. Where potential organic matter sources are isotopically distinct, and when the sources of variation in the natural abundances of stable-isotope ratios of these sources are known, measurements of stable-isotope ratios may help define the appropriate scales of investigation of population, community, and food web dynamics by revealing the spatial extent of the resource base of consumers.

Our results suggest that during productive summer periods, many consumers rely on local sources of production, rather than on production derived from other habitats. In Table 2, we summarize our estimates of the spatial extent of the sources of production supporting river food webs. During summer base flow periods, most invertebrate and vertebrate consumers were dependent on within-habitat sources of algal production. Top predators in the river, steelhead and rainbow trout, were significant exceptions to this pattern of carbon flow (Table 2, Fig. 9). Trout, as well as filter-feeding invertebrates, rely on a wider, and as yet unknown, spatial basis of production.

The reason for the dominance of algal production in shallow pools to trout in other habitats is not fully understood at this time. Preliminary data has shown that algal production rates in riffles and in shallow pools are similar (J. C. Finlay, *unpublished data*). The greater importance of shallow pools may be at least in part due to the greater area of these habitats relative to riffles.

For most ecosystems, the spatial scale of primary production supporting consumers in food webs is likely to be determined by multiple factors, such as habitat productivity, carbon quality, and consumer behavior and mobility. In lotic ecosystems, factors such as geomorphology and discharge may also strongly influence carbon sources to consumers, through effects on transport of organic matter, algal production, and consumer movement. Our research demonstrates the spatial complexity of trophic dynamics in rivers and shows that carbon sources for consumers in the same habitat may be derived from a mix of local and more distant sources (i.e., pools vs. riffles, terrestrial vs. algal) depending on feeding mode or habitat type. For example, during midsummer, black fly ($\delta^{13}C$, -22‰) and blepharicerid

TABLE 2. Summary of estimates of the spatial extent of carbon source areas to river consumers during summer base flows, by consumer habitat (shallow pools, riffles, or deep pools).

Consumer	Carbon source	Spatial extent†
Shallow pools		
Scraper and collector-gatherer taxa	epilithic algae	local
Shredders	epilithic algae and terrestrial detritus	local, upstream forests
Invertebrate predators	epilithic algae	local
Small vertebrates	epilithic algae	local
Juvenile steelhead	epilithic algae	local
Riffles		
Scraper and collector-gatherer taxa	epilithic algae	local
Invertebrate predators	epilithic algae	local, plus upstream shallow pool
Filter feeders	epilithic algae and terrestrial detritus	upstream shallow pools, riffles, forests
Juvenile steelhead	epilithic algae	upstream shallow pools
Deep pools		
Rainbow trout	epilithic algae	shallow pools

† "Local" indicates production derived within the consumer's habitat.

(δ^{13}C, −34 to −31‰) larvae that live within millimeters of each other in the same high-velocity riffle habitats derived different proportions of their carbon from local or upstream pool, riffle, or terrestrial sources.

Carbon flow to top predators

During summer months, stable carbon isotope results showed that algal production in shallow-pool habitats largely supported growth of fish within those pools, as well as trout in downstream riffles and large deep pools (summarized in Fig. 9). These results, along with data for baetid mayfly δ^{13}C in drift samples (Fig. 6), suggest that prey emigration (i.e., movement of invertebrate prey from shallow pools to riffles) was the main trophic link from shallow pools to trout in riffle habitats. Furthermore, we always recaptured fish originally collected in riffles within riffles (J. C. Finlay, *unpublished data*), suggesting limited movement of riffle steelhead to pools during summer base flow periods.

Analysis of δ^{15}N showed that large trout in deep pools represent at least a fourth trophic level in the

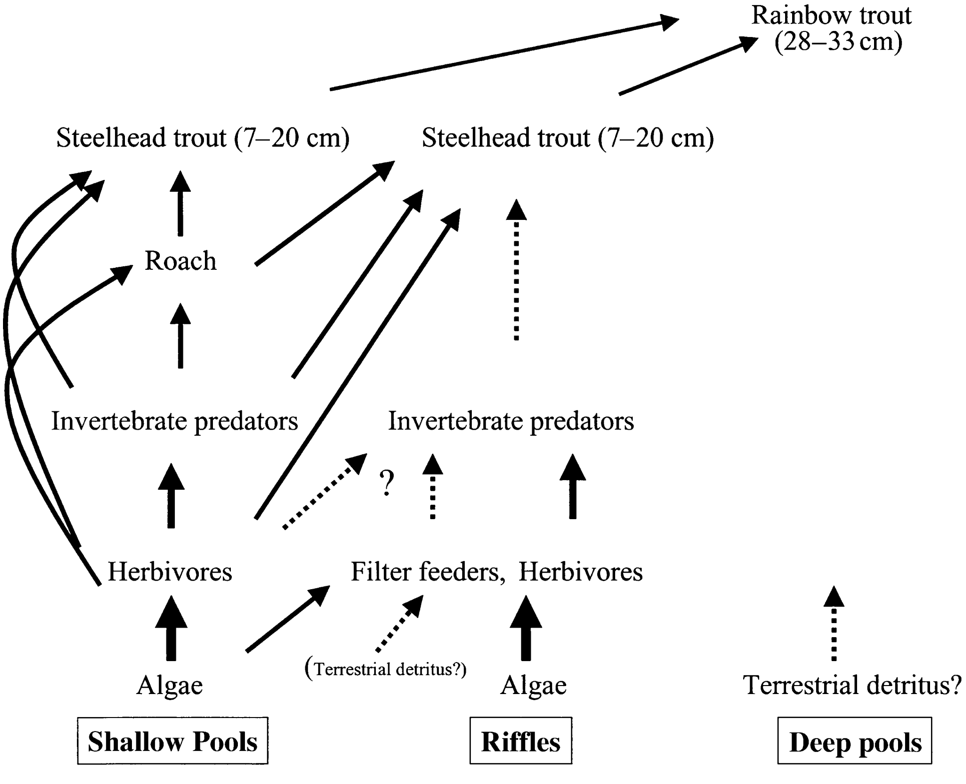

FIG. 9. Food web diagram of carbon flow between consumers in the three main habitats of the South Fork Eel River, California (USA). Solid and dashed lines represent strong and weak trophic connections, respectively.

river. These large individuals in deep pools were probably resident rainbow trout, because juvenile steelhead typically migrate to the ocean at smaller sizes, and because $\delta^{15}N$ values of $\sim$9‰ were too low for these fish to be summer steelhead (i.e., anadromous trout that return to freshwater before sexual maturity; Withler 1966). It is unknown if these fish are genetically similar to steelhead trout, and therefore cannibals, or are reproductively isolated from the juvenile steelhead trout they prey upon.

Carbon sources of these large trout in deep pools appeared to be dominated by algal production derived from shallow pools. We did not measure stable-isotope ratios of potential invertebrate prey in deep pools, but roach and juvenile steelhead trout of the size classes consumed by large trout were never collected or observed foraging in such habitats (J. C. Finlay and M. E. Power, *personal observation*), suggesting that local production in deep pools could not be directly routed to large trout. Thus, the reliance of large trout on shallow pool production must be mediated by movement of fish, either through large trout foraging in shallow pools or riffles, or by some dispersal of juvenile steelhead into deep pools. More information on fish movement is necessary to clarify flow paths of shallow-pool algal production to trout in all habitats.

Previous experiments in the SF Eel River have shown strong effects of juvenile steelhead trout on the structure and dynamics of benthic food webs in shallow pools dominated by *Cladophora* (Power 1990*b*, 1992*b*). All trout data for this study were from 1998, a year when most shallow pools were dominated by epilithic algal films and not *Cladophora*. Our stable-isotope results suggest that the dynamics of shallow pool food webs are critically important to trout production in all habitats of the river. We expect this to be true in years of high *Cladophora* abundance in shallow pools, since this alga provides abundant substrata for epiphytic diatoms and invertebrates (Power 1990*a*, 1992*b*).

Our results show that growth of top predators in rivers may be strongly linked to the production of adjacent river habitats. These results provide further evidence that riffle food webs are open systems with heavy reliance by drift-feeding predators on prey sources from other habitats (Cooper et al. 1990, Dahl 1998, Forrester et al. 1999). Thus, experiments or models examining effects of drift-feeding fishes on river food webs must be done at scales that consider the movement of predators and prey over relatively large scales. While fishes in the river may be affecting invertebrate populations through behavioral or other nonconsumptive mechanisms (e.g., Peckarsky and McIntosh 1998), our results show that effects of predation by fish on invertebrate prey in both shallow pools and riffles should be strongest on shallow-pool invertebrates.

Understanding the sources of production supporting salmonids and other mobile top predators could provide crucial information to guide management of rivers. Steelhead trout, as well as other anadromous salmon species, are declining throughout their range, and the causes of these declines are disputed and poorly understood (Busby et al. 1996, Silvestro 1997). The sources of production for juvenile stages of salmonids are largely unknown, limiting efforts to restore and protect critical habitats in watersheds (Poff and Huryn 1998). In Pacific Coast watersheds, open canopied rivers play a key role for growth or habitat of large size classes of juvenile salmonids (Murphy and Hall 1981, Hawkins et al. 1983, Wilzbach and Hall 1985, Johnson et al. 1986, Leider et al. 1986, Wilzbach et al. 1986). Our results provide clear evidence that salmonid growth in one such river is largely based on algal production.

Conclusions

When variability in natural-abundance stable-isotope ratios in ecosystems is well understood, such measurements help elucidate the patterns and controls of carbon flow in spatially complex food webs. Such information is an essential prerequisite for further basic understanding of population, community, and ecosystem processes, but has largely been unavailable to ecologists and managers. This information is a first step in determining the appropriate scale of experimental investigation for river food web studies. Such information may be useful in protecting and conserving habitats and food webs, including those that support juvenile salmonids.

ACKNOWLEDGMENTS

We thank J. Sabo, S.Yelenik, A. Su, L. Kahn, H. Ames, J. Williams, and J. Fox for help in the field and laboratory, P. Steel and the University of California Natural Reserve System for logistics support, and P. Brooks for assistance with stable-isotope analyses. We thank T. Dawson, C. D’Anontio, C. Harvey, S. Hobbie, J. Sabo, and two anonymous reviews for comments that improved the manuscript. This research was supported by a National Aeronautics and Space Administration Global Change Fellowship, National Science Foundation Division of Environmental Biology Grants (nos. 9615175 and 9901983), and a California Water Resources Grant.

LITERATURE CITED

Adams, T. S., and R. W. Sterner 2000. The effect of dietary nitrogen content on $\delta^{15}N$ enrichment across trophic levels. Limnology and Oceanography **45**:601–607.

Araujo-Lima, C., B. Forsberg, R. Victoria, and L. Martinelli. 1986. Carbon sources for detritivorous fishes in the Amazon Basin. Science **234**:1256–1258.

Ben-David, M., R. W. Flynn, and D. M. Schell. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. Oecologia **111**:280–291.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences **53**:164–173.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. National Oceanographic and

Atmospheric Administration Technical Memorandum NMFS-NWFSC-27.

Calder, J. A., and P. L. Parker. 1973. Geochemical implications of induced changes in ^{13}C fractionation by blue-green algae. Geochimica et Cosmochimica Acta **37**:133–140.

Cifuentes, L. A., M. L. Fogel, J. R. Pennock, and J. H. Sharp. 1989. Biogeochemical factors that influence the stable nitrogen isotope ratio of dissolved ammonium in the Delaware Estuary. Geochimica et Cosmochimica Acta **53**:2713–2721.

Cooper, S. D., S. Diehl, K. Kratz, and O. Sarnelle. 1997. Implication of scale for patterns and processes in stream ecology. Australian Journal of Ecology **23**:27–40.

Cooper, S. D., S. J. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology **71**:1503–1514.

Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. Oecologia **116**:426–432.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta **42**:495–506.

Dodds, W., D. A. Gudder, and D. Mollenhaur. 1995. The ecology of *Nostoc*. Journal of Phycology **31**:2–18.

Doucett, R. R., G. Power, D. R. Barton, R. Drimmie, and R. A. Cunjak. 1996. Stable isotope analyses of nutrient pathways leading to Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences **53**:2058–2066.

Finlay, J. C. 2000. Stable isotope analysis of river food webs and carbon cycling. Dissertation. University of California-Berkeley, California, USA.

Finlay, J. C. 2001. Stable carbon isotope ratios of river biota: implications for carbon flow in lotic food webs. Ecology **82**:1052–1064.

Finlay, J. C. *In press*. Controls of streamwater dissolved inorganic carbon dynamics in a forested watershed. Biogeochemistry.

Finlay, J. C., M. E. Power, and G. Cabana. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnology and Oceanography **44**:1198–1203.

Forrester, G. E., T. L. Dudley, and N. B. Grimm. 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. Limnology and Oceanography **44**:1187–1197.

France, R. L. 1996. Absence or masking of metabolic fractionations of ^{13}C in a freshwater benthic food web. Freshwater Biology **36**:1–6.

Fry, B., and E. B. Sherr. 1984. δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions to Marine Science **27**:13–47.

Golladay, S. W. 1997. Suspended particulate matter concentration and export in streams. Journal of the North American Benthological Society **16**:122–130.

Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences **53**:1370–1381.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540–551.

Hamilton, S. K., W. M. Lewis, and S. J. Sippel. 1992. Carbon sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia **89**:324–330.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences **40**:1173–1185.

Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by δ^{34}S, δ^{13}C, and δ^{15}N. Canadian Journal of Fisheries and Aquatic Sciences **50**:2071–2076.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia **120**:314–326.

Hynes, H. B. N. 1975. The stream and its valley. Verhandlungen, Internationale Vereinigung fur Theoretische und Angewandte Limnology **19**:1–15.

Johnson, S. W., J. Heifetz, and K. V. Koski. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. North American Journal of Fisheries Management **6**:532–537.

Laurance, W. F., R. K. Didham, and M. E. Power. 2001. Ecological boundaries: a search for synthesis. Trends in Ecology and Evolution **16**:70–71.

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Movement and survival of presmolt steelhead in a tributary and the main stem of a Washington River. North American Journal of Fisheries Management **6**:526–531.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399–418.

Mayer, M. S., and G. E. Likens. 1987. The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). Journal of the North American Benthological Society **6**:262–269.

Minigawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta **48**:1135–1140.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clearcut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences **38**:137–145.

Pardue, J. P., R. S. Scalan, C. V. Baalen, and P. L. Parker. 1976. Maximum carbon isotope fractionation in photosynthesis by blue-green algae and a green algae. Geochimica et Cosmochimica Acta **40**:309–312.

Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia **113**:565–576.

Peterson, B. J., B. Fry, L. Deegan, and A. Hershey. 1993. The trophic significance of epilithic algal production in a fertilized tundra river ecosystem. Limnology and Oceanography **38**:872–878.

Phillips, D. L., and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia **127**:171–179.

Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. Canadian Journal of Fisheries and Aquatic Sciences **55**(Supplement 1):210–217.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecological Systems **28**:289–316.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist **147**:396–423.

Power, M. E. 1990*a*. Benthic turfs vs. floating mats of algae in river food webs. Oikos **58**:67–79.

Power, M. E. 1990*b*. Effects of fish in river food webs. Science **250**:811–813.

Power, M. E. 1992*a*. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archives für Hydrobiologie **125**:385–410.

Power, M. E. 1992*b*. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology **73**:1675–1688.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society **7**:503–524.

Rounick, J. S., and B. J. Hicks. 1985. The stable carbon isotope ratios of fish and their invertebrate prey in four New Zealand rivers. Freshwater Biology **15**:207–214.

Rounick, J. S., and M. J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience **36**: 171–177.

Schell, D. M., S. M. Saupe, and N. Haubenstock. 1989. Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by δ^{13}C techniques. Marine Biology **103**:433–443.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience **41**:704–712.

Schlosser, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology **76**:908–925.

Silvestro, R. 1997. Steelhead trout: factors in protection. BioScience **47**:409–414.

Stapp, P., G. A. Polis, and F. S. Pinero. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. Nature **401**:467–469.

Tyus, H. M., W. C. Starnes, C. A. Karp, and J. F. Saunders. 1999. Effects of invasive tissue collection on rainbow trout, razorback sucker, and bonytail chub. North American Journal of Fisheries Management **19**:848–855.

Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. Canadian Journal of Fisheries and Aquatic Sciences **54**:1142–1158.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ^{15}N and δ^{13}C and the trophic position of aquatic consumers. Ecology **80**:1395–1404.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography **48**:2061–2066.

Vannote, R., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**: 130–137.

Wada, E., and A. Hattori. 1978. Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. Geomicrobiology Journal **1**:85–101.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science **277**:102–104.

Webb, S. C., R. E. M. Hedges, and S. J. Simpson. 1998. Diet quality influences the δ^{13}C and δ^{15}N of locusts and their biochemical components. Journal of Experimental Biology **201**:2903–2911.

Wilzbach, M. A., K. W. Cummins, and J. D. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology **67**:898–911.

Wilzbach, M. A., and J. D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. Verhandlungen, Internationale Vereinigung für Theoretische und Angewandte Limnology **22**: 2516–2522.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences **54**:1259–1269.

Withler, I. L. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific Coast of North America. Journal of the Fisheries Research Board of Canada **23**:365–392.