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Carbon Isotope Signatures and Spatial Scales of Energy Flow in food webs
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Project Objectives

Spatial scales of the food webs that support the growth of juvenile salmonids in California rivers are largely unknown, but such information is essential for management of flows, species, and other ecosystem factors influencing salmonid production. Our project objectives were:

1. to determine whether predictable variation in algal $\delta^{13}\text{C}$ with water velocity, and measurements of consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ could be used to examine energy flow and trophic structure in food webs of the South Fork Eel River, and other salmon-bearing streams in Northern California, and
2. to provide this information as a basis for examining how changes in access to energy sources following river regulation or invasions of exotic species might influence the access of various web members, including salmonids, to these sources.

Methods

Site Description

The study was conducted in the forested headwaters of the South Fork (SF) Eel River (140 km² watershed area) in Mendocino County, California, USA (39°44'N, 123°39'W) from spring 1997 to late summer 1999. Along the 3 km study reach, the river has a wide active channel (ca 30 m) with 15 to 45% forest canopy cover. Most precipitation falls between October and May, and discharge declines after winter rains to stable summer baseflows (Figure 1A). The river is warm and productive during the summer months, and water temperature and algal biomass peak in July (Power 1990a, 1992a). During this period, invertebrate assemblages are dominated by collector-gatherer and scraper functional feeding groups (Power 1992a,b). River habitats are composed of long, shallow pools, riffles, and deep (3 to 8 m) pools that have low light penetration. Sampling efforts focused on reaches that were dominated by epilithic algae and had low abundance of filamentous algae.

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 salmon were not observed during the study period from 1997 to 1999 suggesting that marine derived organic matter inputs were not a major source of nutrients to the river during the study periods. Carcasses of anadromous Pacific lamprey (*Lampetra tridentatus*) were more abundant in 1999 than the previous two years, and may have provided additional sources of carbon and nitrogen to the river food web.

Physical and chemical variables

Temperature and pH were measured at least monthly (Orion 540A) at mid afternoon at one site in the middle of the study reaches. Discharge was calculated from stage height data at a gaging station 3 to 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 carbon isotope ratios

Seasonal and spatial variation in algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used to identify sources of production to river food webs. Environmental influences on algal $\delta^{13}\text{C}$ have been previously described in this system (Finlay et al. 1999, Finlay 2000). Briefly, in streams and rivers with canopy cover <90% in the South Fork Eel River watershed and elsewhere in northern California, low supply of dissolved CO₂ (CO_{2(aq)}) relative to photosynthesis rates increase algal $\delta^{13}\text{C}$ in pool

relative to riffle habitats. The amount of ^{13}C -enrichment is negatively related to water velocity. The effect of water velocity on algal $\delta^{13}\text{C}$ changes seasonally with discharge and algal productivity, but long summer periods with stable discharge (Figure 1A) and relatively homogenous water velocities within pool and riffle habitats produce distinct $\delta^{13}\text{C}$ of pool versus riffle algae.

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 (i.e. >3 m depth) were not sampled because we assumed low production in these habitats due to low light penetration.

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 diatoms (i.e. *Achnanthes minutissima*, *Cocconeis* spp., and *Epithemia* spp.) and, to a lesser extent, filamentous green algae (i.e. *Cladophora glomerata*). Cyanobacteria (i.e. *Nostoc pruniforme*) were avoided because of inedibility to most invertebrates at the study site (Dodds et al. 1995).

Samples of 2 to 40 individual larvae were collected with forceps from cobbles for each invertebrate sample. Sampling was conducted in two ways. First, samples for epilithic algae (several samples per site, each sample a composite of 2-3 subsamples) and invertebrates (samples from 3-7 cobbles, composited 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 (i.e. "herbivores") 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 (i.e. shallow near-shore habitats with water velocity <0.03 ms^{-1}) and fast flow (i.e. top surfaces of rocks in fast riffle flows) environments were avoided 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 $\delta^{13}\text{C}$ were determined by water velocity (Finlay et al. 1999), this method of sampling allowed us to assess the foraging range of primary consumers at a finer scale than the first method. Each sample was collected by compositing algae and herbivores from one or two adjacent cobbles with similar water velocity. Water velocity was measured approximately 6 cm above the sampled substrata with a Marsh McBirney flow meter (Model 2000). To characterize algal and invertebrate stable isotope ratios by riffle or shallow pool habitats, as described in 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.

Herbivores sampled 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 (see below). For most invertebrate samples, guts were removed within several hours of collection by dissection and discarded. When dissection was not possible (i.e. for small taxa), larvae were held for 24h without food for gut clearance before rinsing and drying. Samples were dried at 50 °C for ~48h.

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

Samples for stable carbon isotope ratios of suspended particulate organic matter (SPOM) were collected by filtering 0.7 to 1.5 L of river water onto a pre-ashed glass fiber filter (nominal

pore size 0.8 m). Samples of terrestrial detritus were collected for stable isotope analyses from patchy deposits (0.2 to 1 m² area) 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 dried at 50 °C to a constant weight. 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 and epilithic algae were processed and analyzed with methods described previously.

Drift sampling

To measure invertebrate dispersal rates 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 m mesh nets. Samples were preserved in 70% EtOH 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; large roach were fin clipped (see below). For small fishes, stable isotope analyses were done on acid washed, 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 also acid washed prior to grinding and analyses.

We used non-destructive 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 samples periods, epilithic algae were the dominant growth form at most sites, although in late August, several shallow pool sites had 10 to 30% cover of *Cladophora*. Trout were weighed and measured (standard length, SL) and small sections of caudal or anal fins were clipped from each fish. Fin clipping did not appear to be harmful to the performance of the fish (Personal observation; also see Tyus et al. 1999).

Young of year trout (1-5 cm SL) were not routinely sampled in the spring because maternal nitrogen of marine origin obscured trophic position and diet information. Elevated young of year trout $\delta^{15}\text{N}$ (between +12 to 17‰ depending on size; Unpublished data) were similar to adult Pacific salmon $\delta^{15}\text{N}$ reported by Bilby et al. (1996). The marine isotopic signature of maternal steelhead persisted in young trout until individuals were >5 cm 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. 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. $\delta^{13}\text{C}$ are expressed relative to the PDB standard and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. Means for epilithic

algae, herbivores, black flies, Hydropsychid caddisflies, and predators in shallow 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 In press). Riffle and pool algal $\delta^{13}\text{C}$ were distinct from the baseflow period 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 differences between algal and herbivore $\delta^{13}\text{C}$ in pools or riffles (t tests, $P > 0.05$), so we used means of all algae and herbivore $\delta^{13}\text{C}$ values for July in shallow pools ($-18.9 \pm 0.5\text{‰}$) and riffles ($-23.6 \pm 0.5\text{‰}$) for endmembers in the model. We assumed no contribution of terrestrial detritus-based food webs to fish diets (see Results and Discussion). All mean and error estimates were made according to equations from Phillips and Gregg (In press). Fish $\delta^{13}\text{C}$ were corrected for trophic enrichment of $+0.5\text{‰}$ per trophic level. This value is less than the $+1\text{‰}$ 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 $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen 1999).

Findings

Physical and chemical variables

Temperature and pH increased during summer baseflow to mid July maxima (see Fig. 1, Finlay et al., in press). Dissolved $\text{CO}_2(\text{aq})$ 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 FBOM from deposits of terrestrial litter) sampled from shallow pools in summer 1997 and 1998 (see Fig. 2, Finlay et al., in press) were similar to typical values for terrestrial C_3 plants (i.e. -28‰). Leaves were ^{13}C -depleted relative to FBOM as generally observed in stream ecosystems (Finlay In press). We did not measure terrestrial detritus $\delta^{13}\text{C}$ at other times of the year in the SF Eel River but variation in stream-conditioned leaves and shredders in two nearby tributary streams was low ($\pm 2\text{‰}$) over 8 sampling dates during spring, summer and fall periods (Unpublished data). Conditioned leaves and FBOM had low $\delta^{15}\text{N}$ in 1997 ($-0.51 \pm 0.5\text{‰}$ and $-0.47 \pm 0.5\text{‰}$, respectively; mean \pm standard error (SE)) and 1998 ($-1.78 \pm 0.4\text{‰}$ and $1.23 \pm 0.5\text{‰}$ respectively).

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 (1-2 cobbles), herbivore $\delta^{13}\text{C}$ were strongly related to epilithic algal $\delta^{13}\text{C}$, suggesting reliance on local sources of algal production by the dominant functional feeding groups (i.e. scrapers and collector-gatherers) in the river. From June to October, herbivore $\delta^{13}\text{C}$ tracked variation in algal $\delta^{13}\text{C}$ in shallow pool and riffle habitats (see Fig. 3, Finlay

et al., in press). In mid July of 1999, herbivore $\delta^{13}\text{C}$ also tracked small-scale variation in algal $\delta^{13}\text{C}$ (see Fig. 4, Finlay et al., in press) related to water velocity effects on boundary layer thickness around benthic algal cells (Finlay et al. 1999). Similar relationships between herbivore $\delta^{13}\text{C}$ and water velocity were observed on other dates during baseflow periods of 1998 and 1999. Since these samples were collected by compositing algae (July 1999 only) and herbivores (3 dates) from small habitat patches (i.e. adjacent cobbles with similar water velocity), such results indicate that herbivores largely relied on local sources of algal production, consistent with limited mobility of benthic grazers. For the July 1999 results, however, algal $\delta^{13}\text{C}$ were ^{13}C -enriched by about +1‰ on average relative to herbivore $\delta^{13}\text{C}$. This enrichment is inconsistent with potential trophic enrichment of herbivores (0 to +1‰) relative to algae, and may have been due to one of three factors. First, peak pH and unusually low $\text{CO}_2(\text{aq})$ (Finlay 2000) in the river during mid July may have induced a short-term enrichment in algal $\delta^{13}\text{C}$, due to a negative relationship between $\text{CO}_2(\text{aq})$ and algal $\delta^{13}\text{C}$. This enrichment may not have been reflected in herbivore $\delta^{13}\text{C}$ since consumers have longer tissue turnover times than algae. Second, herbivores may have consumed a surface layer of epilithic algae that was ^{13}C -depleted relative to the sampled epilithic matrix. Such depletion could be due to greater access to $\text{CO}_2(\text{aq})$, and thus increased discrimination against ^{13}C , 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. Finally, herbivore $\delta^{13}\text{C}$ may have been influenced by consumption of a small amount of ^{13}C -depleted carbon, such as terrestrial detritus. However, if consumption of terrestrial detritus did contribute slightly to consumer diets, the regression slope of the relationship between water velocity and herbivore $\delta^{13}\text{C}$ should be lower than for the relationship between water velocity and algal $\delta^{13}\text{C}$. In contrast, the slope of water velocity – algae $\delta^{13}\text{C}$ were higher than for the herbivore relationship, suggesting that this third possibility cannot account for the algal ^{13}C -enrichment relative to herbivores in mid July.

Riffle algae and herbivore $\delta^{13}\text{C}$ were consistently depleted relative to pools, and the differences between habitats increased during the summer baseflow period, when $\text{CO}_2(\text{aq})$ was at lowest levels (Finlay 2000). We used consistent differences between shallow pool and riffle algal and herbivore $\delta^{13}\text{C}$ as a natural tracer of algal production derived from each habitat through river food webs during summer baseflow periods when algal $\delta^{13}\text{C}$ were relatively constant between dates.

Algal and herbivore $\delta^{13}\text{C}$ within pools and riffles were also seasonally variable, providing a tracer of algal contributions to river food webs during spring versus summer. In both habitats, herbivore $\delta^{13}\text{C}$ increased from spring to summer, while $\delta^{15}\text{N}$ decreased. Increased summer algal $\delta^{13}\text{C}$ relative to spring values were related to decreased algal fractionation, or discrimination against ^{13}C , and, to a lesser extent, increased $\delta^{13}\text{C}$ of $\text{CO}_2(\text{aq})$ during the productive summer months (Finlay 2000). The decreased herbivore $\delta^{15}\text{N}$ during summer months was probably related to seasonal changes in inorganic nitrogen sources or fractionation by algae (Wada and Hattori 1978, Cifuentes et al. 1988). However, since algal $\delta^{15}\text{N}$ were measured infrequently, decreasing trophic position of riffle “herbivores” (i.e. transition from predation to herbivory by macroinvertebrates thought to be obligate herbivores) from spring to summer cannot be eliminated.

Stable isotope ratios of filter feeders (black flies and Hydropsychid caddisfly larvae) in riffles and invertebrate predators in pools and riffles followed general seasonal patterns of algae and herbivores suggesting at least partial reliance on algal carbon. $\delta^{13}\text{C}$ values for filter feeders were usually intermediate between riffle and pool algal $\delta^{13}\text{C}$, often approaching pool algal $\delta^{13}\text{C}$ values during mid summer. SPOM $\delta^{13}\text{C}$ (-28 to -26‰) were similar to values for terrestrial detritus (i.e. -28‰) and riffle algae. During midsummer, SPOM values were ^{13}C -depleted relative to black fly and Hydropsychid $\delta^{13}\text{C}$, indicating selective feeding on or assimilation of algae in the water column derived from pools by filter feeding invertebrates in riffle habitats. Hydropsychid $\delta^{15}\text{N}$ were usually higher than black fly $\delta^{15}\text{N}$ suggesting predation on drifting invertebrates as well as consumption of particulate organic matter.

Invertebrate predator $\delta^{13}\text{C}$ tracked variation in algal and herbivore $\delta^{13}\text{C}$ in shallow pools but not riffles. On average, riffle predator $\delta^{13}\text{C}$ were ^{13}C -enriched relative to riffle algal or

herbivore $\delta^{13}\text{C}$ by 2‰ ($-25.1 \pm 0.2\text{‰}$ for herbivores versus $-23.1 \pm 0.2\text{‰}$ for predators for all baseflow data, suggesting partial reliance on shallow pool-derived algal carbon through either consumption of herbivores dispersing from pools or filter feeders. Invertebrate predator $\delta^{15}\text{N}$ were usually less than the expected $+3.4\text{‰}$ above herbivore $\delta^{15}\text{N}$. High ($\sim 4\text{‰}$) predator and herbivore $\delta^{15}\text{N}$ were observed in July of 1999 and may have been the result of consumption of lamprey carcasses that were more abundant than during previous years (Personal observations).

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

Drifting invertebrates

Stable carbon isotope ratios of baetid mayflies drifting from shallow pools and riffle habitats were similar to those of algae and herbivores in shallow pools and riffles, respectively, suggesting that dispersing herbivores relied on algal production from the habitat they had departed. Invertebrate predators and roach fry were more abundant in drift samples from shallow pools in July and August.

Vertebrates

Roach, threespined stickleback, and newt $\delta^{13}\text{C}$ in shallow pools were similar to algal and herbivore $\delta^{13}\text{C}$ within these habitats, suggesting strong reliance on local algal carbon (see Fig. 9, Finlay et al., in press). We suggest that carbon sources for these consumers were local (i.e. derived from the pools habitats where consumers were sampled) based on two observations. First, examination of quantitative drift samples indicate that dispersal of invertebrate larvae from riffles into pools is largely dominated by riffle taxa (Unpublished data). Second, $\delta^{13}\text{C}$ of baetid mayflies, common in drift samples throughout the summer period, were consistent with reliance on algal carbon sources in the habitats from which they drifted. These observations suggest that invertebrate drift from upstream shallow pools through riffles and into downstream shallow pools was not important to the diets of small vertebrate predators.

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 $\delta^{13}\text{C}$ (fin = $0.99m + 0.22$, $r^2 = 0.99$) and $\delta^{15}\text{N}$ (fin = $1.04m - 0.26$, $r^2 = 0.97$). In 1999, however, slopes for similar relationships for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significantly different from 1 (Unpublished data) suggesting that such relationships must be assessed annually.

In 1998, summer growth of all size classes of trout in all habitats was largely derived from algal production in shallow pools. For individuals 10 to 15 cm SL, steelhead $\delta^{13}\text{C}$ increased from early June to late August by 4 to 6‰, and $\delta^{15}\text{N}$ decreased by 2 to 3‰ (see Fig. 10, Finlay et al., in press). Low trout $\delta^{13}\text{C}$ and high $\delta^{15}\text{N}$ in June indicate some springtime growth based on invertebrates in pools or riffles, which had ^{13}C -depleted and ^{15}N -enriched stable isotope ratios compared to summer baseflow periods. By late August, however, trout $\delta^{13}\text{C}$ for all size classes in shallow and deep pools, and in riffles closely matched mean algal and invertebrate $\delta^{13}\text{C}$ in pools, although mean trout $\delta^{13}\text{C}$ were slightly lower for riffle trout for the smaller size classes (see Fig. 9, Finlay et al., in press). Using a stable carbon isotope mixing model, we inferred that trout growth in all habitats was highly dependent on algal production in shallow pools (Table 1). Although riffle trout did rely in part on riffle algal production, there was no relationship between riffle trout $\delta^{13}\text{C}$ and riffle area for late August data ($P = 0.24$, $r^2 = 0.08$, $n = 9$; data not shown).

The two-source mixing model results may be sensitive to several of our assumptions. First, we assumed no contribution of terrestrial detritus to fish diets because for the most abundant taxa, variation in invertebrate consumer $\delta^{13}\text{C}$ was explained by variation in algal $\delta^{13}\text{C}$. However, if terrestrial detritus $\delta^{13}\text{C}$ (-28‰ for CPOM in 1998) is used as a mixing model endpoint instead of riffle algae $\delta^{13}\text{C}$, estimated contributions of pool algae to trout diets would be ca. 20%

higher than for the riffle algal $\delta^{13}\text{C}$ endpoint, and terrestrial detritus accounts for a very low percentage of trout diets (i.e. minimum 7.2%, maximum 19.5%, depending on habitat). Although we cannot resolve the contribution of riffle algae versus terrestrial detritus to trout with mixing model calculations, our results demonstrate the contribution of either source is small relative to that of pool algae.

Second, we used algal and herbivore $\delta^{13}\text{C}$ from the period of peak productivity (i.e. mid July) as source endpoints for the model. Algal $\delta^{13}\text{C}$ were more depleted in mid August in both shallow pools ($-19.5 \pm 1.3\text{‰}$, $n=5$; \pm standard deviation) and riffles ($-26.1 \pm 2.3\text{‰}$, $n=5$). Use of these endpoints in the mixing model would result in substantially higher estimates (minimum 88%, maximum 100%) of pool algal contributions to trout diets compared to use of the mid July endpoints.

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 (19 to 24 °C) and productive summer months. Further, trout $\delta^{13}\text{C}$ showed only minor increases with SL in August and such increases are consistent with expected increases in $\delta^{13}\text{C}$ with trophic position (France 1996). If trout were not in isotopic equilibrium with their prey then we would expect larger differences in $\delta^{13}\text{C}$ with size because of differences in tissue turnover times between small and large trout (Hesslein et al. 1993). Therefore this assumption seems reasonable. However, if trout $\delta^{13}\text{C}$ were not at equilibrium with summer prey $\delta^{13}\text{C}$ (that is, increasing from ^{13}C -depleted June values), then trout $\delta^{13}\text{C}$ at equilibrium would be higher than the values used in the model. The use of higher trout $\delta^{13}\text{C}$ values would result in greater calculated contributions of pool algae to trout diets than estimated in Table 1. Thus, based on these three analyses of critical assumptions involved in our calculations, we suggest that the mixing model estimates are conservative with respect to the contribution of pool algae to trout diets.

$\delta^{15}\text{N}$ data showed increased trout trophic position with size. Steelhead trout $\delta^{15}\text{N}$ increased with length, and large rainbow trout (25-32 cm SL) in deep pools had $\delta^{15}\text{N}$ values about 4‰ higher than the smallest size classes of steelhead trout sampled from riffles or shallow pools.

$\delta^{15}\text{N}$ per trophic level (Minigawa and Wada 1984, Vander Zanden et al. 1997), these data suggest cannibalism on smaller size classes of juvenile steelhead and predation on roach by smaller size classes of juvenile steelhead (Personal observation). Large individuals in deep pools were probably resident rainbow trout because juvenile steelhead typically migrate to the ocean at smaller sizes, and because $\delta^{15}\text{N}$ values of ~ 9‰ were too low for these fish to be summer steelhead (i.e. anadromous trout that return to freshwater before sexual maturity; Withler 1966). These large trout were never observed foraging in habitats other than deep pools during the day, although they may have moved undetected into other habitats at night.

Patterns of steelhead stable isotope ratios suggest some contribution of riffle production to the diet of small trout size classes in the spring. For steelhead 7-15 cm SL, spring 1998 $\delta^{15}\text{N}$ were 2-3‰ higher and $\delta^{13}\text{C}$ were 4-6‰ lower than $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, of similar sized fish in August 1998 (see Fig. 12, 13, Finlay et al., in press) or 1997 (Finlay et al. 1999). Increased springtime steelhead $\delta^{15}\text{N}$ may reflect some growth during the winter and spring based on consumption of riffle herbivores ($\delta^{15}\text{N}$ ~ 3.5‰ during spring 1998, Figure 6b). Because invertebrate predators are rare in the spring (Personal observation), riffle herbivore prey more likely account for patterns in steelhead $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Conclusions

1. Analyses of $\delta^{13}\text{C}$ 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.
2. Riffle invertebrate predators also relied in part on consumers of pool-derived algal carbon.

3. One abundant taxon drifting from shallow pools and riffles (baetid mayflies) relied on algal production derived from the habitats from which they dispersed.
4. Trophic linkage from pool algae to riffle invertebrate predators therefore appeared to be mediated through predation on pool herbivores dispersing into riffles, or on filter feeders.
5. 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 these carbon sources appeared to play minor roles for vertebrate consumers.
6. In shallow pools, small vertebrates, including threespined 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.
7. Preliminary data suggest that the strong role of pool algae in riffle steelhead growth during summer periods was due to drift of pool invertebrates to riffles rather than movement of fish. $\delta^{15}\text{N}$ data showed that resident rainbow trout (25-33 cm standard length) in deep pools were cannibalistic on smaller size classes of juvenile steelhead that were most often found in riffles or shallow pools. This connection linked all habitats in the river. 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.
8. Isotope surveys, by revealing energy source areas to consumers in river food webs, can help managers anticipate changes in these sources as water management alters the area or proportion of fast, slow, deep, and shallow habitats in rivers. Knowledge of explicit spatial sources can also help us evaluate food web impacts on species like salmonids of invasions by other species, like squawfish, which are known to displace them from pool habitats (Brown and Moyle 1989).

Publications:

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- Bastow, Finlay, J.C., M.E. Power and G. Cabana. 1999 Effects of carbon limitation on algal carbon isotope ratios: implications for river food webs. *Limnology and Oceanography* 44:1198-1203.
- Finlay, J.C. Stable carbon isotope ratios of river biota: Implication for energy flow in lotic food webs. in press, *Ecology*.
- Jacques C. Finlay, Sapna Khandwala, and Mary E. Power. Spatial Scales of Energy Flow in a River Food Web. *Ecology*, in press.
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