Landscape variation in C sources of scraping primary consumers in streams

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Abstract. We studied variation in C and energy flow in stream food webs by examining primary consumer diets and potential food sources at 8 sites of different drainage areas in the South Fork Eel River drainage. Both heptageniid mayfly nymphs and *Glossosoma* caddisfly larvae are considered scrapers in traditional functional feeding group classification, but past studies suggested that they differed in their relative use of terrestrial and algal C in some streams. In our study, microscopic examination and stable C isotope ratios ($\delta^{13}C$) suggested an increasing contribution of algae to both epilithic biofilms and fine particulate organic matter as stream drainage area and productivity increased. The proportion of algal cells in biofilms of small, unproductive streams was low, and biofilm $\delta^{13}C$ values were similar to those of terrestrial detritus, suggesting that biofilms were composed primarily of heterotrophic microorganisms. *Glossosoma* larvae fed selectively on algae where it was scarce within the biofilms of small forested streams. In contrast, heptageniid mayfly nymphs did not appear to feed selectively on algae, but consumed algae and other materials in proportion to their abundance in the environment. These feeding patterns may have consequences for energy flow through food webs. Heptageniid mayflies feeding on biofilms in unproductive streams may augment the flow of dissolved organic C from terrestrial sources through food webs. In contrast, selective feeding by abundant *Glossosoma* larvae may reduce the flow of algal C through food webs because they are resistant to aquatic predators.

Key words: carbon source, scrapers, diet, food web, epilithon, fine particulate organic matter, *Glossosoma*, Heptageniidae, stable carbon isotopes, Eel River drainage, drainage area.

Algae and terrestrial detritus are the predominant sources of energy available to steam consumers (Jones 1950, Chapman and Demory 1963, Minshall 1967, Cummins 1974, Minshall 1978). In forested drainages, headwater stream food webs often are supported primarily by allochthonous detrital inputs and, as stream size increases, local algal production becomes more important as an energy source (Minshall 1978, Vannote et al. 1980, Hawkins and Sedell 1981, Finlay 2001, Rosi-Marshall and Wallace 2002). This transition probably is driven by higher primary productivity and reduced terrestrial inputs in larger streams (Minshall 1978, Vannote et al. 1980, Benfield 1997, Lamberti and Steinman 1997, Finlay 2004); however, pathways of C flow through food webs responding to these changes are poorly resolved. Such a transition occurs in the South Fork Eel River (California) drainage: top predators are supported by terrestrial detrital C in unproductive streams with drainage area (DA) <10 km², and by local algal C in larger, more productive streams (Finlay et al. 1999, Finlay 2001). Herbivore taxa within a site can differ in their reliance on terrestrial or algal C, and some use algal C in streams where predators are supported by terrestrial C (Finlay 2001).

Many stream primary consumers are adapted to

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feed on organic materials of certain particle sizes and degree of attachment to stream substrates (Cummins 1973, Cummins and Klug 1979). However, the composition of these materials varies spatially and temporally so these adaptations may not predict an animal's diet or indicate if the animal is supported by energy fixed by terrestrial plants or by instream algae (Hynes 1970, Lamberti 1996, Mihuc 1997, Dangles 2002). In forested drainages, the composition and sources of organic materials available to primary consumers change predictably with stream size. Epilithic biofilms may be dominated by algae and algal exudates in open streams and by heterotrophic organisms assimilating terrestrial dissolved organic C (DOC) and their exudates in shaded streams (Findlay et al. 1993, Ledger and Hildrew 1998, Romani and Sabater 1999). The contribution of algal production to fine particulate organic matter (FPOM) is also likely to increase with stream size (Naiman and Sedell 1979, Hawkins and Sedell 1981). These shifts in organic matter composition may result in predictable changes in primary consumers' diets.

Our study focused on the diets of 2 scraping primary consumers: *Glossosoma* caddisfly larvae and nymphs of mayflies in the family Heptageniidae. Previous studies suggested that these taxa might respond differently to shifts in organic matter composition. As in other regions, (Muttkowski and Smith 1929, Jones 1950, Chapman and Demory 1963, Oemke 1984), *Glossosoma* in the South Fork Eel River drainage seem to be algivores (Finlay et al. 1999, Finlay 2004). In contrast, C sources of heptageniids can change with increasing stream size. In small streams (DA. < 10 km^2) these mayflies assimilate a mix of detrital C from terrestrial sources and algal C, with somewhat greater reliance on terrestrial C (J. Finlay, University of Minnesota, personal communication). In larger streams, they assimilate primarily algal C (Finlay 2001). Heptageniid mayflies remove epilithon using brushes on their maxillary and labial palps (McShaffrey and McCafferty 1988, Arens 1989), and genera vary in their proficiency (McShaffrey and McCafferty 1986, 1988). In at least one species, the brushes are not capable of removing biofilms tightly adhering to substrates, and the animals feed primarily on loose detrital particles (McShaffrey and McCafferty 1986), although others species are quite effective scrapers (McShaffrey and McCafferty 1988, Arens 1989).

The purpose of our study was to investigate the mechanisms for variation in scraper diets with stream size. We compared 2 scrapers with different roles in stream food webs: *Glossosoma* caddisfly larvae, which have stone cases that reduce predation (Kohler and McPeek 1989, Parker 1994, Power 1995), and heptage-

niid mayfly nymphs, which are readily eaten by predators (Parker 1994). We hypothesized that *Glossosoma* caddisflies would consume more algae than heptageniid mayflies. We expected that *Glossosoma* diet would not vary substantially with drainage area, but heptageniids would rely more on algae in larger, more productive streams. We hoped to determine whether the relatively high consumption of algae by *Glossosoma* in unproductive streams was the result of selective feeding or efficient scraping. We had 2 hypotheses for why heptageniids might shift to a diet incorporating more algae in larger streams. First, if heptageniids are inefficient scrapers, they might be able to feed only on algae that is loosely attached to the substrate or incorporated into unattached FPOM. Second, heptageniids may be able to remove biofilms, but heterotrophic microorganisms might dominate biofilms in the unproductive streams. By comparing diets with available organic matter, we could better understand the paths through which terrestrial and algal C enter stream food webs.

Methods

Study site

Our study took place close to the headwaters of the South Fork Eel River in the Coast Ranges of northern California, USA (Mendocino County). We sampled 8 sites with DAs of 0.6 km^2 to 145 km^2 (Table 1), including the South Fork Eel River and 6 of its tributaries (Fig. 1). All sites are in or near the University of California's Angelo Coast Range Reserve (lat 39°43′45″N, long 123°38′40″W). The drainage is steep and covered with mixed conifer–hardwood forest dominated by Douglas fir (*Pseudotsuga menziesii*). With the exception of white alder (*Alnus rhombifolia*), the dominant trees are evergreen, so canopy cover over the streams remains relatively constant throughout the year. Aquatic macrophytes are rare, possibly as a result of scouring winter floods (Power 1992). Canopy cover declines (Table 1) and light availability, productivity, and temperature increase with DA within the drainage (Finlay 2004).

Study organisms

We used a combination of gut content and stable C isotope analyses to investigate diets of *Glossosoma* caddisfly larvae and heptageniid mayfly nymphs. We found 4 genera of heptageniid mayflies in the drainage: *Cynigmula*, *Epeorus*, *Nixe*, and *Cynigma*. We focused on *Nixe* and *Cynigma* because they were abundant in pools of multiple streams. Pool algae have stable C isotope ratios (δ^{13}C) that are distinct from

TABLE 1. Study site characteristics. Mean (±1 SE) wetted width was calculated from measurements along 6 transects per site in July 2002. Canopy cover was measured with a spherical densitometer in August 2002.

Stream site	Drainage area (km^2)	Slope (%)	Wetted width (m)	% canopy cover
Skunk	0.6	7.8	0.37 ± 0.12	97
McKinley	0.6	9.0	0.56 ± 0.12	93
Barnwell	2.0	5.5	1.06 ± 0.34	93
Fox	2.9	3.3	1.39 ± 0.15	95
Jack of Hearts	9.9	1.6	2.47 ± 0.32	81
Elder 2	13.5	1.6	3.95 ± 0.85	80
Elder 1	16.9	1.3	4.12 ± 0.39	78
South Fork Eel	145	0.2	7.33 ± 1.50	46

those of terrestrial detritus in most of the study streams (Finlay et al. 1999, Finlay 2004) making differences in diet relatively simple to interpret. We compared the mayflies to the 2 species of *Glossosoma* that were abundant in the drainage: *Glossosoma*

penitum in small tributaries (DA < 10 km^2) and *Glossosoma califica* in larger streams.

Organic matter and insect collection

We collected insects and organic matter from a 100-m-long reach at each study site between 27 July and 27 August 2003. We collected 3 types of organic matter: epilithic biofilms (epilithon), benthic FPOM, and terrestrially derived coarse particulate organic matter (CPOM). Epilithon was organic matter tightly adherent to stones that was not dislodged by gently shaking the stone under water. Benthic FPOM was loose organic material resting on the stream bottom, but not adherent to the substrate. CPOM was conditioned leaves and twigs. We determined δ^{13}C values of all 3 materials, and measured chlorophyll *a* content and ash-free dry mass (AFDM) of epilithon and FPOM. We examined epilithon and FPOM microscopically to determine algal content (see below).

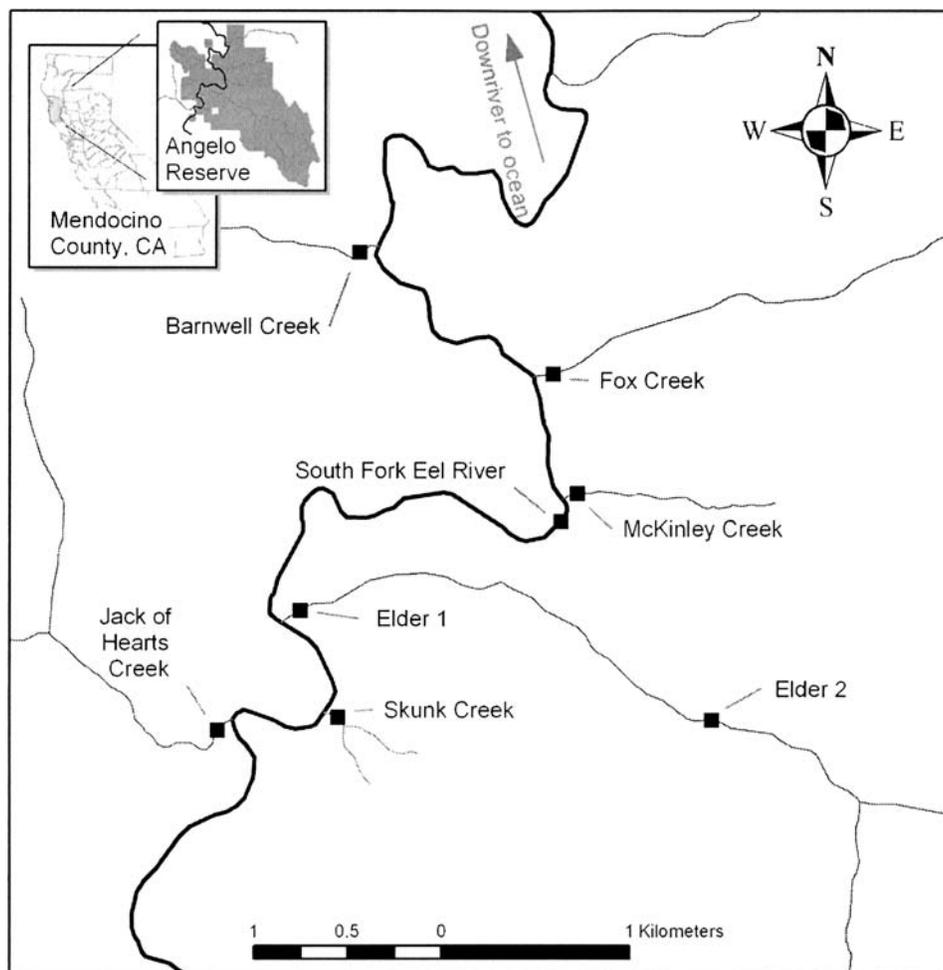We selected 10 stones for epilithon samples (8–25-cm

FIG. 1. Study sites (black boxes) in the South Fork Eel River drainage.

median diameter) haphazardly from each study reach, and collected three 8.2-cm² samples of epilithon from the top of each stone. We used a small wire brush to collect samples for measurement of AFDM and chlorophyll *a*, and a medium toothbrush to collect samples for microscopy. Microscopy samples were preserved in 10% formalin. We collected 6 spatially segregated stable C isotope samples per site by scraping 3 to 10 cobbles per sample (5–25-cm median diameter) with a toothbrush.

We collected 6 evenly spaced FPOM samples from each study reach by removing loose benthic organic matter from the stream bottom with an aspirator. We removed material from a continuous area until enough was accumulated for all analyses, but we did not quantify the areas from which samples were aspirated or determine mean standing crop of FPOM in the streams. We collected FPOM from the surface of the stream bottom, rather than by taking sediment cores, because we expected surface material to be more accessible than material deeper in the sediments to the primary consumers examined. Subsamples for microscopic analysis were preserved in 10% formalin.

$\delta^{13}C$ values of CPOM generally are very similar to the ratios of other forms of terrestrial detrital C in streams (Finlay 2001). Therefore, we collected conditioned leaves and twigs as a baseline for the $\delta^{13}C$ values of terrestrial detrital inputs to the streams. We collected 10 spatially segregated samples of conditioned CPOM from each site by removing leaves and twigs from natural leaf packs and rinsing them in the stream to remove sediment. We inspected them visually and removed any insects, then dried the CPOM at 60°C for ≥48 h.

We collected heptageniid mayfly nymphs from pools at 8 sites and *Glossosoma* caddisfly larvae from pools at 7 sites by removing them from stones with fingers or forceps. *Glossosoma* larvae were not present in pools of the South Fork Eel River. We dissected guts out of larvae, preserved them in 10% formalin, and stored them at 4°C. Tissue other than gut was used to form composite samples (1–7 individual heptageniids or 8–30 *Glossosoma*) for stable C isotope processing. Each isotope sample contained only individuals of the same genus from the same site. When possible, we combined individuals found in close proximity (on same or adjacent stones) and with similar body lengths. Stable isotope samples were dried at 60°C.

Sample processing

We determined chlorophyll *a* and AFDM of epilithon and FPOM. We filtered samples for chlorophyll *a* analysis onto glass-fiber filters (Whatman GF/C,

pore size = 1.2 μm), which were frozen for up to 2 wk prior to chlorophyll extraction. We extracted chlorophyll in 90% acetone for 24 to 36 h in a dark refrigerator and determined chlorophyll *a* concentrations using a fluorometer (Turner Designs TD-700). We filtered AFDM samples onto precombusted glass-fiber filters (Whatman 934AH, pore size = 1.5 μm) and determined AFDM according to standard methods (Steinman and Lamberti 1996).

We examined the composition of epilithic biofilms, benthic FPOM, and insect gut material microscopically. We homogenized each sample of organic material (including gut material) for 30 s using a vortex stirrer, and then removed a subsample and mounted it on a microscope slide using Taft's sucrose (Hershey and Peterson 1996). We determined the relative abundance of mineral particles, vascular plant pieces, algal cells, broken algal cells, and amorphous organic material in each sample using a compound microscope fitted with a Whipple grid at 400× magnification. We counted the material present under grid intersections until we had a representative sample of ≥200 intersections. Animal tissue, fungal cells, and unidentifiable particles occasionally occurred in the samples and, when present, we included these materials in calculations of relative abundance.

We determined the relative amounts of terrestrial and algal C assimilated by consumers by measuring $\delta^{13}Cs$ of epilithon, FPOM, CPOM, and insect tissue collected at the 8 sites. We filtered epilithon onto preweighed and preashed glass-fiber filters, and dried the filters at 60°C for 48 h. We allowed FPOM samples to settle, decanted the supernatant, and dried the concentrated slurry at 60°C for 1 wk (most samples appeared to be dry within 36 h). We acid-washed epilithon and FPOM samples to remove any potential contamination by carbonates by placing them in a sealed container with an open beaker of concentrated HCl for 24 h (Hamilton et al. 1992). After acid-washing, we redried samples at 60°C for 24 h. We did not acid-wash CPOM and insect samples because there was little or no sediment on these materials after they were rinsed, and carbonates are not abundant in these streams (Finlay et al. 1999). We ground insect tissue with a small steel rod and CPOM samples with a Wiley Mill to a fine powder. $\delta^{13}C$ values were determined using a Europa 20–20 continuous flow mass spectrometer at the University of California, Berkeley Center for Stable Isotope Biogeochemistry. $\delta^{13}C$ values are relative to the Pee Dee Belemite standard. Standard deviation of samples run twice was 0.24‰.

We did not use mixing models (e.g., Phillips 2001) to analyze stable isotope data for 2 reasons: 1) we were

not able to measure the $\delta^{13}C$ values of materials contributing C to the organic materials we examined (e.g., pure algae, dissolved organic C) directly, and 2) $\delta^{13}C$ values of herbivores were frequently outside the range of any of the organic matter types. Differences between $\delta^{13}C$ values of an animal and an important food source could arise through fractionation associated with assimilation of food, although such fractionation may be slight in aquatic habitats (Fry and Sherr 1984, France 1996). Differences in $\delta^{13}C$ values of animal tissue and organic matter sources were frequently substantially larger than could be explained by fractionation during assimilation. In some cases, we used analyses of variance (ANOVAs) to compare $\delta^{13}C$ values among organic matter types or between organic matter types and insect tissue to clarify patterns.

Our interpretation of $\delta^{13}C$ data relied on prior work describing sources of variation in algal isotope ratios within the South Fork Eel River drainage (Finlay et al. 1999, Finlay 2001, 2004). The relationship between stream size and $\delta^{13}C$ of pool algae is consistently positive during summer baseflow (Finlay 2001). This positive relationship is the result of both increasing $\delta^{13}C$ of dissolved inorganic C and increasing C limitation of photosynthesis as stream size increases, resulting in reduced fractionation of C isotopes during photosynthesis (Finlay 2004). As a result, $\delta^{13}C$ of algae varies predictably among our study sites. Algae from small, unproductive streams (DA < 5 km²) have $\delta^{13}C$ values that are substantially more negative than terrestrial detritus, whereas algae from larger, more productive streams have $\delta^{13}C$ values that are substantially less negative than terrestrial detritus (Finlay 2001). No single convenient estimate of algal $\delta^{13}C$ throughout the drainage exists, but algal and terrestrial C have distinct $\delta^{13}C$ values at most sites.

Data analysis

We examined variation in composition of organic matter foods within the drainage by comparing chlorophyll *a* concentrations and proportion of algal cells among sites (random factor) and types of organic matter (epilithon and FPOM; fixed factor) using 2-way ANOVA ($\alpha = 0.05$) (Sokal and Rohlf 1995). When variables differed significantly among sites, we used regressions to determine whether organic matter characteristics varied systematically with DA ($\alpha = 0.05$). When the site × type of organic matter interaction term was significant, we compared types of organic matter at each site using orthogonal contrasts (Sokal and Rohlf 1995). We used log transformation for several variables to meet assumptions of ANOVA or to produce linear relationships for

regressions. We used arcsine($\sqrt{}$) transformation for proportional data (Sokal and Rohlf 1995). We used similar analyses to compare herbivore gut contents with types of organic matter and to compare $\delta^{13}C$ values among types of organic matter. We did all statistical analyses with JMP (version 4, SAS Institute, Cary, North Carolina).

Results

Organic matter composition

Composition of potential insect foods (epilithon and benthic FPOM) varied considerably among sites. In general, the contribution of algae to these materials (as measured by chlorophyll *a* concentration and proportion of algal cells) increased with DA (Fig. 2A–D). Epilithon from the smallest streams in the survey (DA < 1 km²) contained very little algae (<10%; Fig. 2A). Epilithon from the South Fork Eel River, the largest and most productive stream site, also contained relatively little algae compared to other productive streams, indicated by the low proportion of algae (10.3%, Fig. 2A) and low chlorophyll *a* concentrations (Fig. 2B). When this site was included in the analyses, the regression between chlorophyll *a* content or proportion of algal cells and DA was not significant. When this site was excluded, chlorophyll *a* content increased with DA and there was a marginally non-significant trend for the proportion of algae to increase with DA (without South Fork Eel River: arcsine[$\sqrt{}$proportion algae] = $0.222 + 0.195 \times \log_{10}[DA]$), $F = 5.001$, $r^2 = 0.50$, $p = 0.076$, $n = 7$; $\log_{10}[\mu g$ chlorophyll a/mg AFDM] = $-2.618 + 0.323 \times \log_{10}[DA]$), $F = 14.601$, $r^2 = 0.75$, $p = 0.012$, $n = 7$; Fig. 2A, B). Chlorophyll *a* concentration and proportion of algal cells showed that algal content of FPOM also increased with stream size (with South Fork Eel River: arcsine[$\sqrt{}$proportion algae] = $0.116 + 0.239 \times \log_{10}[DA]$, $F = 38.969$, $r^2 = 0.87$, $p = 0.0008$, $n = 8$; μg chlorophyll a/mg AFDM = $0.000283 + 0.000346 \times \log_{10}[DA]$, $F = 17.211$, $r^2 = 0.74$, $p = 0.006$, $n = 8$; Fig. 2C, D). These relationships were more consistent than those observed for epilithon.

Benthic FPOM appeared to contain less living algae than epilithic biofilms. Chlorophyll *a* expressed per mg organic matter (AFDM) was approximately an order of magnitude higher in epilithon than FPOM (Table 2, Fig. 2B, D). The proportion of algal cells was greater in epilithon than in FPOM at most sites, but this difference was not significant except in the South Fork Eel River (Tables 2, 3). Most algae (75–100% of algal cells) in both FPOM and epilithon were diatoms. Most other particles in epilithon and FPOM were amorphous organic matter (71–98% of all particles for epilithon and 60–93% of all particles for FPOM).
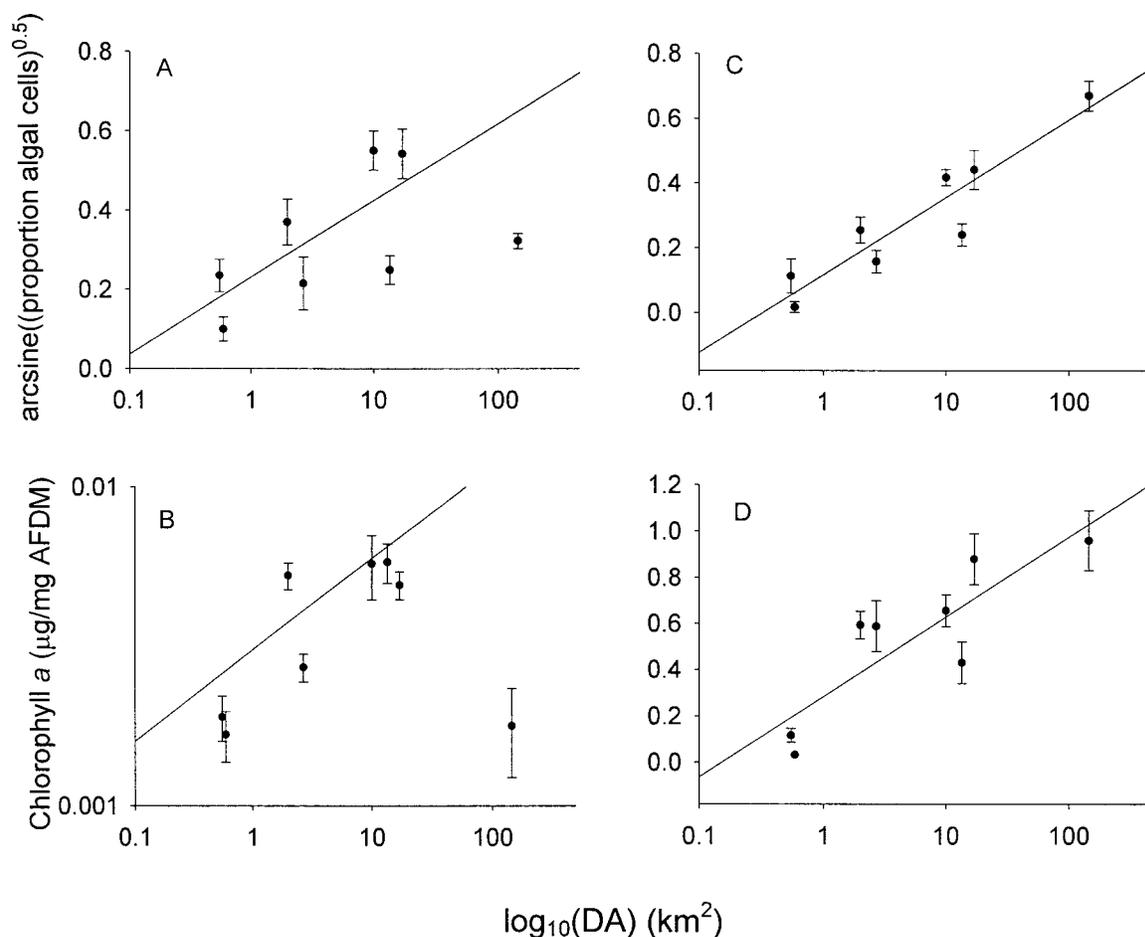
Fig. 2. Relationships between organic matter characteristics and drainage area (DA). A.—Proportion of algal cells in epilithon. B.—Chlorophyll *a* content of epilithon. C.—Proportion of algal cells in fine particulate organic matter (FPOM). D.—Chlorophyll *a* content of FPOM. Regression lines for epilithon exclude the South Fork Eel River. Regression lines for FPOM include all sites. Points are means (±1 SE).

Patterns in $\delta^{13}C$ supported the results of chlorophyll and microscopic analyses. In the smaller streams (DA < 10 km^2), $\delta^{13}C$ for the 3 types of organic matter (epilithon, FPOM, and CPOM; Fig. 3) ranged from −26 to −31, similar to terrestrial plant materials (Fig. 3). In more productive streams, $\delta^{13}C$ of epilithon and FPOM suggest a greater contribution of algae. In 3 streams, epilithon was more ^{13}C enriched than CPOM by ~6 to 9‰ (Fig. 3). Sites where we observed $\delta^{13}C$ for epilithon that was indicative of algal C also had abundant algae

TABLE 2. Analysis of variance results for differences in chlorophyll *a* (/mg organic matter [AFDM]) and proportion of algal cells among sites and types of organic matter (epilithon and fine particulate organic matter) in the South Fork Eel drainage. * = $p < 0.05$, ** = $p < 0.001$.

Dependent variable	Source of variation	SS	df	MS	F
Chlorophyll *a*	Site	13.1	7	1.87	30.5**
	Type of organic matter	24.6	1	24.6	35.3**
	Site × type of organic matter	4.88	7	0.698	11.4**
	Error	6.87	112	0.0613	
Proportion of algal cells	Site	2.94	7	0.421	28.2**
	Type of organic matter	0.0296	1	0.0296	0.317
	Site × type of organic matter	0.655	7	0.0935	6.27**
	Error	1.61	108	0.0149	

TABLE 3. Within-site comparisons using orthogonal contrasts of chlorophyll *a* content and proportion of algal cells between epilithon and benthic fine particulate organic matter (FPOM). n = number of samples, ** = $p < 0.001$.

Site	Chlorophyll *a*			Proportion of algal cells		
	Epilithon (n)	FPOM (n)	F	Epilithon (n)	FPOM (n)	F
Skunk	10	6	88.5**	9	6	1.90
McKinley	10	6	155**	9	6	0.994
Barnwell	10	6	52.7**	10	6	1.83
Fox	10	6	27.4**	9	6	0.895
Jack of Hearts	10	6	42.6**	10	6	2.10
Elder 2	10	6	78.7**	10	6	0.140
Elder 1	10	6	33.9**	10	5	1.51
South Fork Eel	10	6	1.04	10	6	5.50**

in microscopic counts and high chlorophyll content (Figs 2, 3). Biofilms and FPOM from the South Fork Eel River (DA = 145 km^2) had more positive δ^{13}C values than CPOM as well, suggesting that algae contributed much of the C in these materials (Fig. 3).

δ^{13}C of epilithon, FPOM, and CPOM in streams with DA < 10 km^2 were all within the range expected for terrestrial plant C, but δ^{13}C values differed among the 3 types of organic matter (2-way ANOVA, site: $F = 1.455$, $p = 0.235$; organic matter type: $F = 22.318$, $p = 0.0021$, interaction: $F = 4.271$, $p = 0.001$; Fig. 3). Epilithon δ^{13}C tended to be slightly lower than CPOM δ^{13}C (~1‰), and FPOM δ^{13}C tended to be slightly more enriched than CPOM and epilithon δ^{13}C (2–3‰).
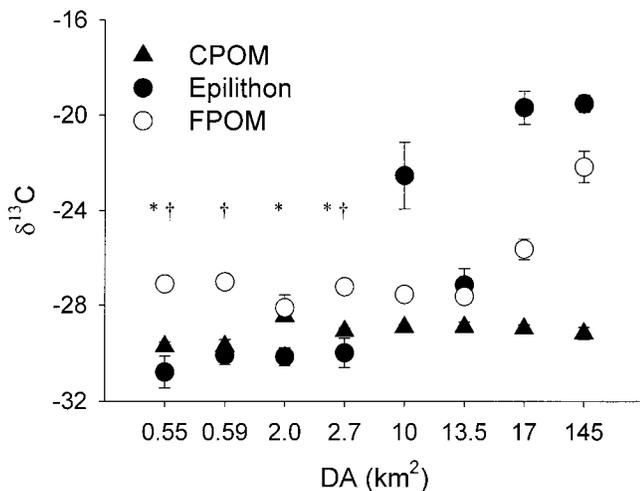

FIG. 3. Mean (±1 SE) stable carbon isotope ratios (δ^{13}C) of coarse particulate organic matter (CPOM), epilithon, and benthic fine particulate organic matter (FPOM) from 8 sites with differing drainage area (DA) in the South Fork Eel River drainage. Among streams with DA < 10 km^2, * indicates sites where δ^{13}C of epilithon and CPOM differed and † indicates sites where δ^{13}C of FPOM and CPOM differed. Larger streams were not included in this analysis.

Insect diets

Glossosoma larvae appeared to be specialist feeders on algae. Algal cells made up 8.5% to 38% of the material in their guts (Fig. 4A). The relative abundance of algae in *Glossosoma* guts differed significantly among sites ($F = 6.262$, $p < 0.0001$, 7 sites, 45 individuals), but this variation was not related to DA. Algae were more abundant in *Glossosoma* guts than in epilithon in small streams, but this difference diminished with increasing stream size (2-way ANOVA, site: $F = 16.9$, $p < 0.001$; material type: $F = 11.4$, $p = 0.014$; interaction: $F = 2.18$, $p = 0.051$; Fig. 4A). The proportion of algae was substantially higher in *Glossosoma* guts than in FPOM at most sites (data not shown).

δ^{13}C values of *Glossosoma* in small, unproductive streams (DA < 10 km^2) were markedly lower than δ^{13}C values of epilithon (by ≥5‰), indicating that *Glossosoma* selectively assimilate some component of the biofilms (Tables 4, 5, Fig. 5A). δ^{13}C for *Glossosoma* in the smallest streams (DA < 1 km^2) was lower than δ^{13}C of *Glossosoma* in slightly larger streams (DA = 2–3 km^2). In larger, more productive streams, *Glossosoma* δ^{13}C values were closer to those observed for epilithon (Fig. 5A). *Glossosoma* tissue in one productive stream (DA = 17 km^2) was less enriched in ^{13}C than epilithon.

Heptageniid mayflies consumed less algae than *Glossosoma*, and their diets were more variable among sites. The dominant genera of heptageniids changed as stream size increased. However, the 2 dominant heptageniid genera in pools (*Nixe* and *Cynigma*) had similar diets when collected from the same sites (2 streams with DA = 2–3 km^2, 2-way ANOVA with site and genus, arcsine√[proportion algae]; site: $F = 0.521$, $p = 0.477$, genus: $F = 0.162$, $p = 0.753$, interaction: $F = 0.0052$, $p = 0.943$). These taxa were combined for further analyses because their diets did not differ significantly. Heptageniids tended to eat more algae in larger streams, but the trend was marginally non-
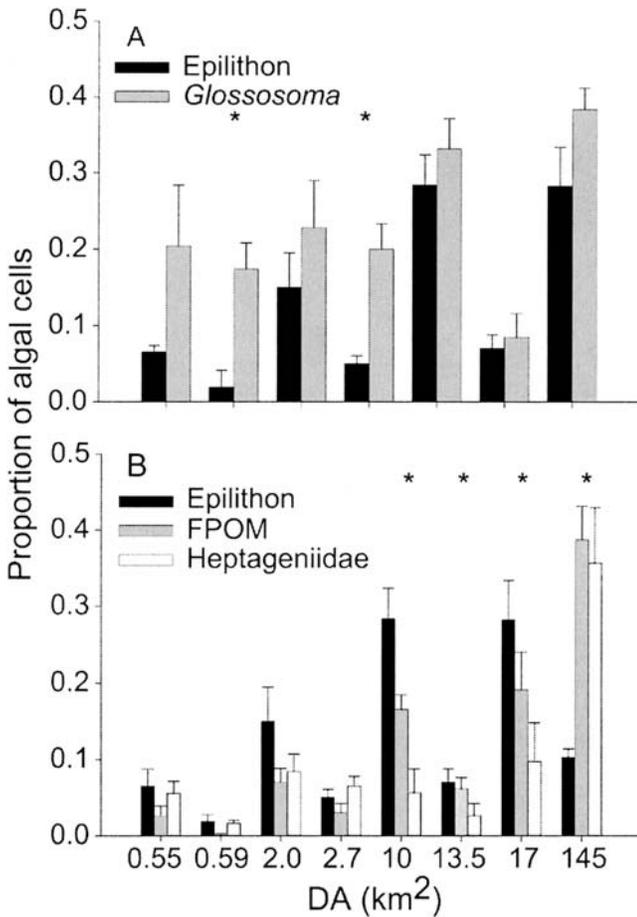
FIG. 4. Mean (+1 SE) proportion of algal cells in insect gut material and organic matter from 8 sites with differing drainage area (DA) in the South Fork Eel River drainage. A.— Proportion of algal cells in epilithon and *Glossosoma* guts. B.—Proportion of algal cells in epilithon, fine particulate organic matter (FPOM), and heptageniid mayfly guts. * indicates sites where the relative abundance of algae differed significantly ($p < 0.05$) between *Glossosoma* or Heptageniid guts and epilithon.

significant (arcsine$\sqrt{}$[proportion algae] $= 0.158 + 0.099 \times \log_{10}$[DA], $F = 4.76$, $r^2 = 0.44$, $p = 0.072$, $n = 8$). In the 4 small tributaries, the proportion of algal cells in heptageniid guts tended to be intermediate between proportions observed for epilithon and FPOM, but the proportion of algal cells did not differ among guts and epilithon (2-way ANOVA, site: $F = 10.4$, $p < 0.001$; material type: $F = 2.43$, $p > 0.2$; interaction: $F = 5.74$, $p < 0.001$) or FPOM (Fig. 4B). In most of the larger tributaries, the proportion of algal cells was lower in mayfly gut material than in either type of organic matter (Fig. 4B). Examination of gut materials did not clarify whether mayflies relied more on epilithon or FPOM. No evidence for consistent selectivity for or against algae was found. Mayfly tissue δ^{13}C generally was distinct from FPOM δ^{13}C but similar to epilithon δ^{13}C (Tables 4, 5, Fig. 5B), although it was slightly more negative than epilithon in 3 streams. *Nixe* δ^{13}C and *Cynigma* δ^{13}C did not differ in the 2 streams where they co-occurred (δ^{13}C, site: $F = 0.466$, $p = 0.506$, genus: $F = 2.780$, $p = 0.344$, interaction: $F = 0.935$, $p = 0.350$), so they were combined for this analysis.

Discussion

Variation in composition of organic food matter

We observed substantial variation in composition of organic matter food and insect herbivore diet within the Eel River drainage. Variation in heptageniid mayfly diet appeared to track variation in the composition of organic matter, whereas *Glossosoma* caddisfly diet was less variable among sites. Heptageniids appeared to feed on epilithic biofilms, and *Glossosoma* appeared to feed selectively on algae.

Epilithon and FPOM composition varied among streams. Biofilms in small unproductive streams contained primarily terrestrial C and little algae. We observed low proportions of algal cells in microscopic

TABLE 4. Analysis of variance results for differences in stable C isotope ratios (δ^{13}C) among sites and types of organic matter (insect tissue and epilithon or fine particulate organic matter [FPOM]) in the South Fork Eel drainage. * $= p < 0.05$, ** $= p < 0.001$.

Type of organic matter	Source of variation	SS	df	MS	F
Glossosoma/epilithon	Site	1926	6	321.0	107.5**
	Type of organic matter	335	1	335.3	10.230**
	Site × type of organic matter	230	6	38.3	12.840**
	Error	152	51	2.85	
Heptageniidae/epilithon	Site	2892	7	413	129**
	Type of organic matter	43.0	1	43.0	6.65*
	Site × type of organic matter	45.2	7	6.46	2.01
	Error	337	118	3.20	
Heptageniidae/FPOM	Site	1234	7	176	73.2**
	Type of organic matter	9.47	1	9.47	0.177
	Site × type of organic matter	374	7	53.4	22.2**
	Error	294	122	2.41	

TABLE 5. Within-site comparisons using orthogonal contrasts of stable C isotope ratios ($\delta^{13}C$) between types of organic matter (insect tissue and epilithon or fine particulate organic matter [FPOM]). n = number of samples, * = $p < 0.05$, ** = $p < 0.001$.

|	Glossosoma vs epilithon			Heptageniidae vs epilithon			Heptageniidae vs FPOM		
Site	Glossosoma (n)	Epilithon (n)	F	Heptageniidae (n)	Epilithon (n)	F	Heptageniidae (n)	FPOM (n)	F
Skunk	1	6	5.69**	9	6	1.43	9	6	5.82**
McKinley	6	5	9.73**	8	5	2.78*	8	6	7.01**
Barnwell	6	6	4.05**	11	6	0.836	11	6	1.62
Fox	8	5	2.57*	7	5	0.144	7	6	3.02**
Jack of Hearts	6	6	1.52	15	6	1.120	15	6	5.32**
Elder 2	6	4	3.68**	10	4	0.472	10	6	0.024
Elder 1	6	5	4.02**	15	5	3.19*	15	6	4.11**
South Fork Eel				16	6	2.57*	16	6	4.00**
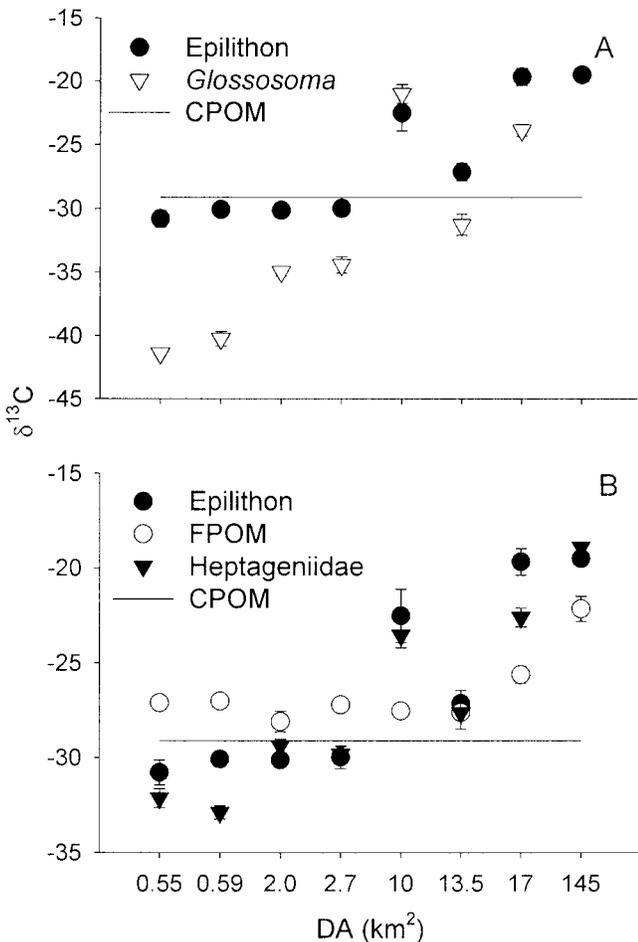
FIG. 5. Mean (±1 SE) stable carbon isotope ratios ($\delta^{13}C$) of *Glossosoma* larvae (A) or heptageniid mayfly nymphs (B) and coarse particulate organic matter (CPOM), epilithon, and fine particulate organic matter (FPOM) collected from 8 sites with differing drainage area (DA) in the South Fork Eel River drainage. For clarity, $\delta^{13}C$ of CPOM is plotted as a line representing the mean value for all sites.

counts, low chlorophyll *a* concentrations, and $\delta^{13}C$ values close to those of terrestrial plants for these biofilms. Algae in these streams are likely to be substantially depleted in ^{13}C compared to terrestrial plants since dissolved inorganic C (DIC) in these streams is relatively depleted in ^{13}C (Finlay 2001, 2003, 2004). In addition, DIC is abundant compared to demand, allowing strong discrimination against ^{13}C in uptake of DIC during algal photosynthesis (Finlay 2004). Both of these mechanisms result in algal $\delta^{13}C$ values that are substantially depleted in ^{13}C compared to algae of more productive streams or terrestrial plants (Finlay 2004). $\delta^{13}C$ values of biofilms in unproductive streams suggest that biofilms may be made up largely of terrestrially derived organic C—probably heterotrophic organisms supported by DOC and their exudates. Algal contribution to epilithic biofilms in the South Fork Eel River drainage generally increased with DA; chlorophyll *a* and the proportion of algal cells within the biofilms increased with DA when the South Fork Eel River itself was excluded from the analysis. Although chlorophyll *a* content and proportion of algal cells in South Fork Eel River biofilms were surprisingly low, biofilms had enriched $\delta^{13}C$ values as would be expected for C-limited pool algae in this productive stream (Finlay et al. 2002, Finlay 2004).

Why was algal biomass so much lower in the South Fork Eel River than would be expected for a stream of its size? The South Fork Eel River experiences episodes of algal growth and senescence during the summer growing season, and large mats of filamentous *Cladophora glomerata* are often abundant (Power 1992). We did not include *Cladophora* in epilithon samples; heptageniids generally do not live in the *Cladophora* mats and probably cannot feed on it because their mouthparts would have difficulty shearing the thick filaments (McShaffrey and McCafferty 1986, 1988, Arens 1989). However, *Cladophora* may exude DOC that is taken up by epilithic bacteria

(Haack and McFeters 1982, Kaplan and Bott 1989, Romani and Sabater 1999). Therefore, the relatively low abundance of algae in epilithon probably does not reflect the true contribution of algal production and C to biofilms at this site. Sloughed epiphytic algae growing on *Cladophora* and senescent filaments also may contribute to FPOM (Power 1992). High chlorophyll *a* content and abundant algal cells in FPOM, as well as stable isotope data, suggest that algae made a relatively high contribution to FPOM at this site.

Both epilithon and FPOM in unproductive sites have $\delta^{13}C$ values indicative of terrestrial detrital C, but FPOM was enriched in ^{13}C compared to CPOM, and epilithon was depleted in ^{13}C compared to CPOM. Finlay (2001) also observed that benthic FPOM was enriched in ^{13}C compared to terrestrial CPOM in small streams where such enrichment was unlikely to have been caused by contributions of algal C to FPOM. FPOM probably contains much partially disintegrated terrestrial CPOM that has been decomposed or eaten by shredders (Boling et al. 1975, Wallace et al. 1982, Webster and Benfield 1986). Once masticated to fine particles, FPOM usually contains a higher abundance of bacteria than CPOM, whereas CPOM generally hosts more fungi than FPOM (Findlay et al. 2002). In contrast, detrital C in epilithon probably is a consequence of biofilm-forming bacteria taking up DOC from the water column (Claret and Fontvieille 1997, Hall and Meyer 1998). The more-negative $\delta^{13}C$ of epilithon compared to CPOM probably reflects the presence of some algal C. Differences in C sources or microbial processes may have led to the observed differences in the $\delta^{13}C$ values of epilithon, FPOM, and CPOM in small streams. We do not know the mechanisms creating variation in $\delta^{13}C$ among different classes of organic matter, but this subtle variation was useful in tracing food sources used by insects.

Variation in herbivore diets among sites

Variation in insect herbivore diets was related to variation in the composition of different organic matter sources within the drainage. *Glossosoma* caddisfly larvae appeared to feed selectively on algae when algae was not abundant within epilithic biofilms and to consume or assimilate algal C selectively relative to its contribution to biofilms. Algivory by *Glossosoma* across a range of sites was reflected by both $\delta^{13}C$ values and gut-content analysis. At one site (Elder 2) where *Glossosoma* larvae had low proportions of algal cells in their guts (8.5%), they may have been relatively hungry, as less total material was recovered from their guts than from similar-sized larvae collected at other sites (JME, personal observation). $\delta^{13}C$ values of

Glossosoma tissues in unproductive sites were distinct from those of epilithon, indicating selective feeding or assimilation. As in previous studies (Finlay 2001, 2004), *Glossosoma* $\delta^{13}C$ followed spatial patterns that were well correlated with factors expected to control algal $\delta^{13}C$. These patterns suggest that *Glossosoma* $\delta^{13}C$ is similar to algal $\delta^{13}C$ (which was not measured directly because of the difficulty of separating materials within biofilms). Previous examinations of gut material found that *Glossosoma* fed primarily on algae (Jones 1950, Chapman and Demory 1963, Anderson and Bourne 1974), and an ^{15}N tracer study found that *Glossosoma* selectively assimilated N from a rapidly cycling component of biofilms, probably growing algae (Rezanka and Hershey 2003).

In contrast to *Glossosoma*, heptageniid mayfly nymphs did not selectively consume algae. They consumed algae in proportion to its availability in organic matter (epilithon or FPOM) in unproductive streams, and consumed slightly less algae than available in these materials in productive streams. $\delta^{13}C$ values suggest that they primarily fed on epilithon and assimilated epilithic C—algal or detrital. Another heptageniid, *Stenomena*, has $\delta^{13}C$ values similar to bulk epilithon in some streams (Mulholland et al. 2000, Hamilton et al. 2004), and some heptageniids selectively assimilate heterotrophic bacterial C (Edwards and Meyer 1990, Hall 1995, Hall and Meyer 1998). Feeding on heterotrophic biofilms by heptageniids or other scrapers that do not selectively feed on algae may be an important pathway by which terrestrial detrital C enters stream food webs (Warren et al. 1964, Benke et al. 1992, Hall 1995, Hall and Meyer 1998, Fuller et al. 2004).

The differences in diet between the 2 herbivores, both classified as scrapers in traditional functional feeding groups (Cummins and Klug 1979), appear to be the result of selective feeding by *Glossosoma* larvae rather than of inefficiency of heptageniid feeding on biofilms. Heptageniids may feed on more algae than other primary consumers in small unproductive streams because they are able to feed effectively on biofilms. *Glossosoma* appear to feed selectively on algae even when algae are scarce in biofilms. Increased reliance by heptageniids on algal production in larger, more productive streams appears to be the result of greater contribution of algae and algal C to epilithic biofilms, rather than of increased availability of loose or detrital algae.

Understanding the differences in C and energy sources used by herbivores and the mechanisms leading to shifts in herbivore C sources should help resolve why C sources to stream food webs shift along productivity and stream-size gradients (Power and

Rainey 2000, Power and Dietrich 2002). Heptageniid mayflies in small unproductive streams appear to augment flows of terrestrial detrital C to food webs by feeding on heterotrophic biofilms supported by DOC. Heptageniid mayflies are readily consumed by local predators (Parker 1994). Selective grazing on algae by *Glossosoma* larvae may deplete biofilms of algae and reduce its availability to heptageniid nymphs and other consumers. As a result, relatively inedible stone-cased *Glossosoma* larvae may reduce flows of algal C through instream food webs. Both of these animals are abundant and can contribute a large fraction of total invertebrate biomass in the streams. *Glossosoma* larvae make up 15 to 50% of the invertebrate biomass of Fox Creek (McNeely 2004) and are abundant in tributaries of the South Fork Eel River (densities range from 3 to 1400/m^2; McNeely 2004). Heptageniid nymphs make up 10% of the benthic biomass in Fox Creek (McNeely 2004) and 51% of the benthic biomass of the South Fork Eel River (CM, unpublished data).

We found that combining microscopic analyses of diets and organic matter foods with stable C isotope tracer studies was more effective in elucidating mechanisms of C flow to herbivores than either method alone. Stable C isotope analysis allowed us to infer the origin (terrestrial or algal) of C in organic matter available as food to herbivores. Isotope data showed that potential food sources, as well as heptageniid diets, contained more algal C in larger, more productive streams. Microscopic analysis of organic materials and gut contents confirmed these patterns and allowed us to determine whether mismatches between stable isotope ratios of organic materials and animal tissue were the result of selective feeding. Further work is needed to establish whether algae-poor biofilms in the small, unproductive streams are maintained by DOC-supported bacteria and to understand how predator diets, as well as those of herbivores, influence shifts in energy flow with increasing stream size and productivity.

Acknowledgements

Literature Cited

ANDERSON, N. H., AND J. R. BOURNE. 1974. Bionomics of three species of caddis flies (Trichoptera: Glossosomatidae) in Oregon. Canadian Journal of Zoology 52:405–411.

ARENS, W. 1989. Comparative functional morphology of the mouthparts of stream animals feeding on epilithic algae. Archiv für Hydrobiologie Supplementband 83:253–354.

BENFIELD, E. F. 1997. Comparison of litterfall input into streams. Journal of the North American Benthological Society 16:104–108.

BENKE, A. C., F. R. HAUER, D. L. STITES, J. L. MEYER, AND R. T. EDWARDS. 1992. Growth of snag-dwelling mayflies in a blackwater river: the influence of temperature and food. Archiv für Hydrobiologie 125:63–81.

BOLING, R. H., E. D. GOODMAN, J. A. VAN SICKLE, J. O. ZIMMER, K. W. CUMMINGS, R. C. PETERSEN, AND S. R. REICE. 1975. Towards a model of detritus processing in a woodland stream. Ecology 56:141–151.

CHAPMAN, D. W., AND R. L. DEMORY. 1963. Seasonal changes in the food ingested by aquatic larvae and nymphs in two Oregon streams. Ecology 44:140–146.

CLARET, C., AND D. FONTVIEILLE. 1997. Characteristics of biofilm assemblages in two contrasted hydrodynamic and trophic conditions. Microbial Ecology 34:49–57.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183–206.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. BioScience 24:631–641.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

DANGLES, O. 2002. Functional plasticity of benthic macroinvertebrates: implications for trophic dynamics in acid streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1563–1573.

EDWARDS, R. T., AND J. L. MEYER. 1990. Bactivory by deposit-feeding mayfly larvae (*Stenonema* spp.). Freshwater Biology 24:453–462.

FINDLAY, S., K. HOWE, AND D. FONTVIEILLE. 1993. Bacterial-algal relationships in streams of the Hubbard Brook Experimental Forest. Ecology 74:2326–2336.

FINDLAY, S., J. TANK, S. DYE, H. M. VALETT, P. J. MULHOLLAND, W. H. MCDOWELL, S. L. JOHNSON, S. K. HAMILTON, J. EDMONDS, W. K. DODDS, AND W. B. BOWDEN. 2002. A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. Microbial Ecology 43:55–66.

FINLAY, J. C. 2001. Stable-carbon-isotope ratios of river biota:

implications for energy flow in lotic food webs. Ecology 82:1052–1064.

FINLAY, J. C. 2003. Controls of streamwater dissolved inorganic carbon dynamics in a forested watershed. Biogeochemistry 62:231–252.

FINLAY, J. C. 2004. Patterns and controls of lotic stable carbon isotope ratios. Limnology and Oceanography 49:850–861.

FINLAY, J. C., S. KHANDWALA, AND M. E. POWER. 2002. Spatial scales of carbon flow in a river food web. Ecology 83:1845–1859.

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.

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 in Marine Science 27:13–47.

FULLER, R. L., B. P. KENNEDY, AND C. NIELSEN. 2004. Macroinvertebrate responses to algal and bacterial manipulations in streams. Hydrobiologia 523:113–126.

HAACK, T. K., AND G. A. MCFETERS. 1982. Nutritional relationships among microorganisms in an epilithic biofilm community. Microbial Ecology 8:115–126.

HALL, R. O. 1995. Use of a stable carbon isotope addition to trace bacterial carbon through a stream food web. Journal of the North American Benthological Society 14:269–277.

HALL, R. O., AND J. L. MEYER. 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology 79:1995–2012.

HAMILTON, S. K., W. M. LEWIS, JR, AND S. J. SIPPEL. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia (Berlin) 89:324–330.

HAMILTON, S. K., J. L. TANK, D. R. RAIKOW, E. R. SILER, N. J. DORN, AND N. E. LEONARD. 2004. The role of instream vs allochthonous N in stream food webs: modeling the results of an isotope addition experiment. Journal of the North American Benthological Society 23:429–448.

HAWKINS, C. P., AND J. R. SEDELL. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology 62:387–397.

HERSHEY, A. E., AND B. J. PETERSON. 1996. Stream food webs. Pages 511–530 in F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, UK.

JONES, J. R. E. 1950. A further ecological study of the river Rheidol: the food of common insects of the main-stream. Journal of Animal Ecology 19:159–174.

KAPLAN, L. A., AND T. L. BOTT. 1989. Diel fluctuations in bacterial activity on streambed substrata during vernal algal blooms: effects of temperature, water chemistry, and habitat. Limnology and Oceanography 34:718–733.

KOHLER, S. L., AND M. A. MCPEEK. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology 70:1811–1825.

LAMBERTI, G. A. 1996. The role of periphyton in benthic stream food webs. Pages 533–572 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). Algal ecology. Freshwater benthic ecosystems. Academic Press, San Diego, California.

LAMBERTI, G. A., AND A. D. STEINMAN. 1997. A comparison of primary production in stream ecosystems. Journal of the North American Benthological Society 16:95–104.

LEDGER, M. E., AND A. G. HILDREW. 1998. Temporal and spatial variation in the epilithic biofilm of an acid stream. Freshwater Biology 40:655–670.

MCNEELY, C. 2004. Herbivore responses to stream size gradients in a northern California watershed. PhD Dissertation, University of California, Berkeley, California.

MCSHAFFREY, D., AND W. P. MCCAFFERTY. 1986. Feeding behavior of Stenacron interpunctatum (Ephemeroptera: Heptageniidae). Journal of the North American Benthological Society 5:200–210.

MCSHAFFREY, D., AND W. P. MCCAFFERTY. 1988. Feeding behavior of Rithrogenia pellucida (Ephemeroptera:Heptageniidae). Journal of the North American Benthological Society 7:87–99.

MIHUC, T. B. 1997. The functional trophic role of lotic primary consumers: generalist vs. specialist strategies. Freshwater Biology 37:455–462.

MINSHALL, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48:139–149.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28:767–771.

MULHOLLAND, P. J., J. L. TANK, D. M. SANZONE, W. M. WOLLHEIM, B. J. PETERSON, J. R. WEBSTER, AND J. L. MEYER. 2000. Food resources of stream macroinvertebrates determined by natural-abundance stable C and N isotopes and a ^{15}N tracer addition. Journal of the North American Benthological Society 19:145–157.

MUTTKOWSKI, R. A., AND G. M. SMITH. 1929. The food of trout stream insects in Yellowstone National Park. Roosevelt Wild Life Annals 2:241–263.

NAIMAN, R. J., AND J. R. SEDELL. 1979. Benthic organic matter as a function of stream order in Oregon. Archiv für Hydrobiologie 87:404–422.

OEMKE, M. P. 1984. Interactions between a stream grazer and the diatom flora. Pages 291–299 in J. C. Morse (editor). Proceedings of the 4th International Symposium on Trichoptera. Dr W. Junk, The Hague, The Netherlands.

PARKER, M. S. 1994. Feeding ecology of stream-dwelling Pacific Giant Salamander larvae (Dicamptodon tenebrosus). Copeia 1994:705–718.

PHILLIPS, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia (Berlin) 127:166–170.

POWER, M. E. 1992. Hydrologic and trophic controls of

seasonal algal blooms in northern California Rivers. Archiv für Hydrobiologie 125:385–410.

POWER, M. E. 1995. Floods, food chains, and ecosystem processes in rivers. Pages 52–60 *in* C. G. Jones and J. H. Lawton (editors). Linking species and ecosystems. Chapman and Hall, New York.

POWER, M. E., AND W. E. DIETRICH. 2002. Food webs in river networks. Ecological Research 17:451–471.

POWER, M. E., AND W. E. RAINEY. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291–314 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart (editors). Ecological consequences of habitat heterogeneity. Blackwell Scientific, Oxford, UK.

REZANKA, K. M., AND A. E. HERSHEY. 2003. Examining primary producer–consumer interactions in a Lake Superior tributary using ^{15}N-tracer, grazer-reduction, and nutrient-bioassay experiments. Journal of the North American Benthological Society 22:371–387.

ROMANI, A. M., AND S. SABATER. 1999. The effect of primary producers on the heterotrophic metabolism of a stream biofilm. Freshwater Biology 41:729–736.

ROSI-MARSHALL, E. J., AND J. B. WALLACE. 2002. Invertebrate food webs along a stream resource gradient. Freshwater Biology 47:129–141.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. Freeman, New York.

STEINMAN, A. D., AND G. A. LAMBERTI. 1996. Biomass and pigments of benthic algae. Pages 295–313 *in* F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

VANNOTE, R. L., 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.

WALLACE, J. B., J. R. WEBSTER, AND T. F. CUFFNEY. 1982. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia (Berlin) 53:197–200.

WARREN, C. E., J. H. WALES, G. E. DAVIS, AND P. DOUDOROFF. 1964. Trout production in an experimental stream enriched with sucrose. Journal of Wildlife Management 28:617–660.

WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.