GRAZER TRAITS, COMPETITION, AND CARBON SOURCES TO A HEADWATER-STREAM FOOD WEB

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Abstract. We investigated the effect of grazing by a dominant invertebrate grazer (the caddisfly *Glossosoma penitum*) on the energy sources used by other consumers in a headwater-stream food web. Stable isotope studies in small, forested streams in northern California have shown that *G. penitum* larvae derive most of their carbon from algae, despite low algal standing crops. We hypothesized that the caddisfly competes with other primary consumers (including mayflies) for algal food and increases their reliance on terrestrial detritus. Because *Glossosoma* are abundant and defended from predators by stone cases, their consumption of algal energy may reduce its transfer up the food chain. We removed *Glossosoma* (natural densities >1000 caddisflies/m^2) from five (~4 m^2) stream sections during the summer of 2000 and measured responses of algae, invertebrate primary consumers, and invertebrate predators. The treatment reduced *Glossosoma* biomass by 80–90%. We observed a doubling in chlorophyll *a* per area in sections with reduced *Glossosoma* abundance and aggregative increases in the biomass of undefended primary consumers. Heptageniid mayfly larvae consumed more algae (as measured by stable carbon isotope ratios and gut content analysis) in caddisfly removal plots at the end of the 60-day experiment, although not after one month. We did not see isotopic evidence of increased algal carbon in invertebrate predators, however. Patterns of caddisfly and mayfly diets in the surrounding watershed suggested that mayfly diets are variable and include algae and detrital carbon in variable proportions, but scraping caddisflies consume primarily algae. Caddisfly and mayfly diets are more similar in larger, more productive streams where the mayflies assimilate more algae. Isotopic analysis, in combination with measurements of macroinvertebrate abundance and biomass in unmanipulated plots, suggested that a substantial portion of the invertebrate community (>50% of biomass) was supported, at least partially, by local algal carbon during midsummer. These data suggest that algae may be more important to community dynamics in headwater streams than their relatively low productivity would suggest. Through their high densities and relative invulnerability to predation, armored grazers may also affect community structure and flow of algal and detrital carbon in headwater streams.

Key words: algae; armored grazer; caddisfly; competition; detritus; diet; energy flow; food web; Glossosoma; *headwater stream; mayfly; stable carbon isotopes.*

INTRODUCTION

The relative importance of terrestrial detritus vs. in-stream primary production for supporting stream food webs has been an important question in stream ecology for more than 30 years. In small, forested headwaters, most carbon enters the stream as terrestrial detritus (Fisher and Likens 1973, Webster and Meyer 1997). As stream size increases, algal productivity increases and consumption of terrestrial inputs diminishes (Vannote et al. 1980, Bott et al. 1985, Naiman et al. 1987, Finlay 2001, Rosi-Marshall and Wallace 2002). As a result, as stream size increases there is a transition from secondary production driven by terrestrial inputs to secondary production driven by algae, in many watersheds (Finlay 2001, Rosi-Marshall and Wallace 2002).

While terrestrial carbon strongly dominates organic-matter budgets of forested headwater streams, the small standing biomass of algae relative to detritus may belie its importance to stream consumers. For example, *Neophylax aniqua* caddisflies in Bear Brook (New Hampshire, USA) derive an estimated 75% of their nutrition from algae, despite very low primary productivity (Mayer and Likens 1987). *Glossosoma nigrior* feed almost entirely on diatoms in a heavily shaded Michigan (USA) stream (Oemke 1984). Grazing *Elimia* snails in first-order Walker Branch (Tennessee, USA) make up 95% of invertebrate biomass (Newbold et al. 1983).

Despite the clear importance of algae to some primary consumers in small, shaded streams, this resource is consumed by a limited set of taxa (Rounick et al. 1982, Finlay 2001), often dominated by armored grazers.

Armored grazers, including snails (Gastropoda: Pleuroceridae), stone-cased caddisfly larvae (Trichoptera: Limnephiloidea and Glossosomatidae), and neotropical armored catfishes (Loricariidae) are widespread and frequently abundant (Brown 1991, Wiggins 1996, Power 2003). Some predators are adapted to feed on these animals (e.g., Sadzikowski and Wallace 1976, Mittlebach 1984, McNeely 1987, Harvey and Marti 1993), but they are avoided by most headwater predators (Kohler and McPeek 1989, Parker 1994).

Primary consumers that are less defended from predators do consume algae in headwaters (Rounick et al. 1982, Finlay 2001, McCutchan and Lewis 2002), but use of algal carbon by those consumers in northern California headwaters (where this study was conducted) is limited compared to that of grazing caddisflies (Finlay 2001). For example, carbon isotope ratios of heptageniid mayflies are intermediate between terrestrial detritus and algae in small tributaries (drainage areas ranging from 0.5 to 2.8 km^2) and similar to those of caddisflies and algae in larger, more productive streams (drainage areas equal to 17 km^2 and 140 km^2; Finlay [2001]). Similar assemblages of heptageniids are found across a gradient of stream size (McNeely et al., in press), suggesting that larvae in the smaller streams could use algal food if it were more available and that the larvae may compete with caddisflies for algae. Other undefended primary consumers in small tributaries rely on terrestrial carbon or on a mix of terrestrial and algal carbon, and many shift to a more algal diet in larger streams (Finlay 2001).

Competition between armored grazers and other primary consumers could play a role in limiting the availability of algae to predators in headwater streams. Armored grazers are very effective in limiting algal growth and competing for algal food (McAuliffe 1984, Hawkins and Furnish 1987, Kohler 1992, Steinman 1996). By competing with more vulnerable primary consumers, armored grazers can divert algal productivity away from predators. For example, Dicosmoecus gilvipes, a stone-cased caddisfly, sequesters algal carbon in productive stream reaches, preventing transfer to juvenile salmonids through more edible grazers (Tait et al. 1994, Power et al. 1996, Wootton et al. 1996).

Most studies of armored grazer herbivory and competition have been conducted in unshaded streams with high algal productivity (e.g., McAuliffe 1984, Feminella and Resh 1991, Kohler 1992). Although studies have shown that armored grazers can limit algal growth in less-productive stream reaches (Power 1984, Steinman 1992, Rosemond et al. 1993), the role of these consumers in headwater food webs is poorly known compared to their role in autotrophic streams. Because the amount of carbon fixed by algal production in light-limited headwater streams is generally very low compared to terrestrial inputs (Fisher and Likens 1973, Webster and Meyer 1997), the trophic role of terrestrial detritus in small streams has been strongly emphasized, while algivory by headwater consumers has received less attention. Competition with armored grazers for algae, however, could make other headwater-stream consumers, including those vulnerable to predators, more reliant on terrestrial energy sources. We hypothesized that abundant armored caddisfly larvae compete with more predator-vulnerable primary consumers for algal resources and thus reduce the transfer of algal production to predators. We investigated this hypothesis in a small, heavily shaded tributary of the South Fork Eel River in northern California. We predicted that Glossosoma penitum, a common cased caddisfly in small streams, would outcompete other stream primary consumers, including mayflies, midges, and beetle larvae, for algae, increasing reliance of these primary consumers and their predators on energy derived from terrestrial detritus. We tested this hypothesis by removing Glossosoma larvae from sections of the creek and monitoring macroinvertebrate responses. We measured changes in both biomass and diet (using stable carbon isotopes and direct observations) of primary consumers and invertebrate predators. Where we reduced Glossosoma densities, we expected to see greater consumption and assimilation of algal carbon by other invertebrate consumers. We expected increased assimilation of algal carbon by primary consumers as they grew and developed in caddisfly exclusions.

STUDY SITE

Fox Creek (latitude 39°43′45″ N, longitude 123°38′40″ W) is a small tributary of the South Fork Eel River within the Angelo Coast Range Reserve, a 3059-ha protected research reserve in the University of California Natural Reserve System. Draining 2.8 km^2, the ~3 m wide bankfull channel has step–pool morphology (Montgomery and Buffington 1993). Discharge is approximately an order of magnitude higher in winter and early spring than in late summer (C. McNeely, unpublished data). Old-growth mixed hardwood–conifer forest dominated by Douglas fir (Pseudotsuga menziesii) surrounds the stream. Our study area began 100 m upstream of Fox Creek's confluence with the South Fork Eel River and extended 500 m upstream. Canopy cover (measured with a spherical densiometer; Lemmon [1957]) was 95% (for June 2000, percentage open was 5.2% ± 1.9% (mean ± SE)). Evergreen trees and drought deciduous trees (which drop leaves in response to the summer dry season) shed litter into the channel throughout the summer (C. McNeely, unpublished data). As a result, litter abundance is relatively high during the summer. Litterfall is highest in autumn, but high flows in late fall and winter flush these inputs relatively quickly (C. McNeely, unpublished data). Algal standing crops are low, as were summer DOC concentrations (~0.8 mg/L, Finlay 2003). The substrate is mostly boulders (31%) and cobbles (28%), with gravel (22%), pebbles (15%), and some bedrock (3%). Mean inundated width in midsummer 2000 was 0.90 ± 0.33 m (mean ± SD), mean depth was 9.4 ± 5.2 cm, and mean flow was

0.12 ± 0.12 m/s. Stream temperatures are highest in August (~16°C at midday). The top predators in the stream are juvenile steelhead trout (*Oncorynchus mykiss*) and Pacific giant salamander larvae (*Dicamptodon tenebrosus*) (Parker 1992). *Glossosoma penitum* densities average ~1000/m², and biomass peaks in August. The caddisfly is bivoltine with a winter cohort and one or more summer asynchronous cohorts (Teague et al. 1985).

METHODS

Experimental design

To investigate the effects of *Glossosoma penitum* on the Fox Creek food web, we removed *Glossosoma* larvae from five 3 m long stream sections (plots) between June and October 2000. Each plot included the entire width of the channel. We chose five pairs of plots so as to minimize variation in physical conditions. One plot of each pair was randomly assigned to the removal treatment, and the other served as an unmanipulated control. Individual plots within pairs were either adjacent, or separated by no more than 8 m of stream, if separating the plots was necessary to avoid small waterfalls and interference with other research in the stream. Pairs of plots were within 20–100 m of each other. The upstream and downstream ends of each plot were delimited with a low aluminum fence (6 cm high) covered with plastic sheeting coated with petroleum jelly to reduce *Glossosoma* immigration. There was at least 10 cm stream flow over fences at the stream thalweg. We observed salamanders and juvenile steelhead swimming over fences, and we believe drifting invertebrates could have crossed them easily. We repeated removals three times within the first 10 days, beginning 27 June, then once per week for the duration of the experiment. All response variables were measured before beginning removals and one and two months after the initial removal. We used paired *t* tests to compare response variables between the two treatments. We computed plot means for response variables when we collected multiple samples per plot at each sampling interval and used these means for statistical tests, so that plot was the unit of replication for all tests.

Glossosoma *density and biomass*

We determined densities of *Glossosoma* larvae before the start of the experiment and once per month afterwards. Before initiating removals, we counted and measured the case lengths of all *Glossosoma* larvae in entire control plots. Thereafter, we surveyed larvae in a 0.5 m wide transect in each plot (controls and removals). To estimate *Glossosoma* biomass, we regressed case length and individual biomass. In June 2000, we collected 193 *Glossosoma* larvae representing all instars from Fox Creek and measured their case length to the nearest millimeter in the field. We killed them with sodium citrate (Johnston and Cunjak 1999), dried their bodies for 48 h at 50°C, and weighed them to the nearest

0.001 mg with a microbalance (Mettler-Toledo model AT201, Toledo, Ohio, USA). We applied the regression ln (mass (mg)) $= -10.323 + 0.478$ case length (mm) ($P <$ 0.0001, $r^2 = 0.85$; lengths ranged from 1 to 12 mm) to estimate *Glossosoma* biomass in each plot.

Algal and invertebrate biomass

To examine effects on the food web, we monitored algae, as chlorophyll *a*, and invertebrate biomass and composition. To provide a consistent sampling unit, we placed cobbles in the stream in March 2000, 2.5 months before our first sampling. We collected clean, rounded cobbles (12–20 cm median diameter, mean mass 2.5 kg) from nearby dry rock bars on the South Fork Eel River. We placed 18 cobbles, divided into three sampling groups of six cobbles each, in each plot. The three groups had similar cumulative surface area and were marked by a spot of colored paint on each stone. We haphazardly interspersed the groups on the stream bottom within plots. The cobbles were placed to fit within the natural substrate topography. We sampled invertebrates and algae from one group of six stones in each plot prior to initiating the removals (sampling 14–18 June), 30 and 60 days after completing removals (8–9 August and 7–8 September). To sample algae, we scrubbed an 8.2-cm² area of the top of the stone with a wire brush. We kept samples in a dark refrigerator and processed them within 24 hours. We filtered a known fraction of each sample onto a glass fiber filter (pore size 1.2 μm) and extracted it in 90% buffered (1 mg MgCO₃/L) acetone for 24 hours in the dark. We determined chlorophyll *a* concentration using a fluorometer (Sequoia Turner model 112, Testwave LLC, Sparks, Nevada, USA).

To sample invertebrates, we placed a D-frame net (250 μm mesh) downstream of a cobble, then moved it quickly into the net. We removed all invertebrates from the net and stone and preserved them in 75% ethyl alcohol. We identified organisms to genus (except for Chironomidae and Oligochaeta) and measured body lengths to the nearest 0.1 mm. Within the otherwise algivorous or detritivorous Chironomidae, we identified predaceous Tanypodinae to subfamily. Invertebrate biomass was estimated using length–mass regressions (equations and sources are listed in the Appendix). Stone surface area was estimated by wrapping stones in calibrated aluminum foil and weighing the foil (Steinman and Lamberti 1996). We calculated mean invertebrate biomass per stone surface area for each plot.

We classified the invertebrate community into six guilds: (1) armored grazers (animals feeding on algae and protected from predators by substantial cases), (2) vulnerable primary consumers (animals feeding on algae or detritus and not well defended from predation), (3) invertebrate predators, (4) detritivores (animals feeding on coarse particulate organic matter (CPOM)), (5) filterers, and (6) Chironomidae. Guild assignments were based on published information (Merritt and Cummins

1996), previous stable isotope studies (Finlay et al. 1999, Finlay 2001), predation studies in the South Fork Eel River watershed (Parker 1992, 1994), and natural history observations. The Appendix contains a list of taxa assigned to each guild. We separated Chironomidae because we did not identify them below family and could not separate them into guilds (e.g., filterers vs. primary consumers). We compared the biomass of the vulnerable primary consumer and invertebrate predator guilds between treatments. We did not measure responses of juvenile steelhead or Pacific giant salamander larvae, as we expected these animals to range over areas larger than the experimental plots. It is possible that predation by these vertebrates could have masked experimental responses by their invertebrate prey. There was no reason to expect initial differences in their biomass between treatments, however.

Diet and stable isotope analyses

We used stable carbon isotope analysis to determine the relative amounts of terrestrial and algal carbon assimilated by consumers. Tissues of aquatic consumers have ratios of ^{13}C to ^{12}C (expressed relative to a standard as $\delta^{13}C$) that are very similar to those of their assimilated food (DeNiro and Epstein 1978, France 1996). Primary producers are variable in $\delta^{13}C$ due to variation in sources of inorganic carbon (LaZerte and Szalados 1982) and factors affecting discrimination against ^{13}C during photosynthesis (Farquhar et al. 1982, Lathja and Marshall 1994, MacLeod and Barton 1998, Finlay 2004). Analysis of stable carbon isotope ratios in tissues of primary producers and consumers has been used to track assimilation of basal resources through many aquatic food webs (e.g., Rounick et al. 1982, Fry and Sherr 1984). Previous work in Fox Creek (Finlay et al. 1999, Finlay 2001) demonstrated that algae and terrestrial plant detritus differ in their stable carbon isotope ratios, allowing us to track algal and detrital carbon through the food web.

Because invertebrate densities were low, we collected only one sample for stable carbon isotope analysis per plot for each taxon analyzed. We collected a single composite sample of each taxon by haphazardly overturning naturally occurring cobbles throughout the plot until we had enough material (2 mg dry mass, 3–8 cobbles per plot). In June (premanipulation) and August (30 days postmanipulation) we collected samples of *Glossosoma* larvae (15–30 individuals per composite sample), mayfly larvae from the family Heptageniidae (as a representative vulnerable primary consumer, *Nixe* and *Cinygma* spp., 5–12 per sample), stonefly larvae in the family Perlidae (*Hesperoperla* sp., 1–5 per sample), and conditioned terrestrial leaves (leaves colonized by microbes, decomposing in the stream). Heptageniid mayflies were selected because they were abundant, appeared to use both terrestrial and algal carbon (Finlay 2001), and were readily consumed by local vertebrate and invertebrate predators (Parker 1992, 1994). In

September (60 days postmanipulation) we also collected beetle larvae (family Psphenidae, *Eubrianax* sp., 3–10 per sample). These animals were not common earlier in the summer. We dissected guts from the insects and dried samples for 48 hours at 50°C. We preserved guts in 10% formaldehyde. Stable isotope samples were analyzed on a PDZ Europa Scientific 20-20 continuous flow isotope ratio mass spectrometer at the University of California Berkeley Center for Stable Isotope Biogeochemistry (California, USA). Values of $\delta^{13}C$ are relative to the Pee Dee Belemnite Standard.

To determine if consumers' use of algal carbon responded to our manipulation, we compared $\delta^{13}C$ of consumers collected in removal and control plots. Grazing caddisfly larvae (*Neophylax, Glossosoma*) appear to closely track the $\delta^{13}C$ of epilithic algae in the South Fork Eel River watershed (Finlay 2001), and stable carbon isotope ratios (all values given as mean ± SE) of these taxa in Fox Creek are substantially lower than terrestrial detritus or the animals that feed on it. From Finlay et al. (1999), terrestrial CPOM $\delta^{13}C$ = −27.5‰ ± 0.2‰, shredders $\delta^{13}C$ = −26.4 ‰ ± 0.1‰; from our data, *Glossosoma* $\delta^{13}C$ = −35.8 ‰ ± 0.4‰, conditioned leaves $\delta^{13}C$ = −28.3 ‰ ± 0.1‰. The high ratio of supply of inorganic carbon relative to low photosynthetic demand in headwater streams leads to the strong preferential uptake of ^{12}C by autotrophs (Finlay 2001). This high photosynthetic fractionation, together with the low values for $\delta^{13}C$ of dissolved inorganic carbon, produce ^{13}C-depleted $\delta^{13}C$ values of epilithic algae relative to terrestrial organic matter in headwater streams of the South Fork Eel watershed such as Fox Creek (Finlay 2004). If consumers incorporated more algal carbon into their tissues where *Glossosoma* were removed, we would expect their $\delta^{13}C$ to decrease relative to control plots. We did not analyze stable isotope ratios of epilithic algae directly because our attempts to separate algae from biofilms (using methods of Hamilton et al. 2005) were unsuccessful. We estimated the percentage of algal carbon in mayfly and beetle larval tissue with mixing models (Phillips 2001), using two different assumptions about the value of algal $\delta^{13}C$ and the carbon sources of *Glossosoma* caddisflies: (1) *Glossosoma* assimilate only algae, and their tissue reflects algal $\delta^{13}C$ perfectly; or (2) *Glossosoma* assimilate 50% detritus and 50% algae. The assimilated diet of *Glossosoma* is likely to lie somewhere between these proportions based on gut content analysis (McNeely et al., *in press*) and assimilation efficiencies (Cummins 1969, 1975).

To complement stable isotope data, we examined *Glossosoma* and heptageniid gut contents from September samples. We dissected out guts and homogenized their contents with a Vortex stirrer. We mounted a few microliters of the sample on a slide using Taft's medium and examined it at 400× magnification (Jones 1968, Hershey and Peterson 1996). We determined the relative abundance of intact diatoms, green algae, blue-green

TABLE 1. Mean biomass (with SE reported in parentheses) of benthic macroinvertebrates and chlorophyll *a* from experimental plots in Fox Creek, California, USA, in 2000.

	June		August		September			
Guild	Control	Removal	Control	Removal	Control	Removal	*t*	*P*
Macroinvertebrates (mg/m^2)								
Glossosoma	252.0 (8.6)		440 (68)	49.2 (6.3)	272 (49)	46.4 (7.9)	−4.031	0.0079
Vulnerable primary consumers	36.1 (11.6)	29.7 (12.9)	24.8 (5.6)	29.0 (9.0)	38.4 (11.7)	63.3 (23.9)	4.325	0.0062
Heptageniidae	14.1 (3.1)	16.4 (3.0)	16.0 (4.7)	16.2 (5.9)	17.4 (7.7)	23.3 (5.5)	1.753	0.077
Predators	31.3 (27.3)	0.76 (0.41)	23.9 (9.4)	17.4 (3.6)	11.4 (3.2)	36.5 (11.3)	1.954	0.062
Perlidae	30.7 (27.6)	0.073 (0.073)	10.4 (6.9)	6.7 (4.9)	3.7 (3.4)	26.8 (11.5)	1.547	0.098
Chironomidae	0.90 (0.19)	1.06 (0.15)	7.3 (1.2)	7.7 (3.0)	29.1 (14.5)	48.2 (27.3)	0.562	0.302
Chlorophyll *a* (μg/cm^2)	0.88 (0.11)	0.95 (0.26)	1.55 (0.54)	3.40 (0.63)	2.07 (0.41)	3.72 (0.73)	2.75	0.025

Notes: Data are means of 5 plots/treatment. *Glossosoma* biomass was estimated from visual surveys; data for invertebrates and chlorophyll are from benthic stone samples. The treatment effect was tested by a one-tailed paired *t* test of log-transformed biomass on five paired control and *Glossosoma* removal plots. In August, *Glossosoma* had greater biomass in control plots ($t = -5.592$, $P = 0.0025$), and there was more chlorophyll *a* in removal plots ($t = 2.92$, $P = 0.021$).

algae, broken diatoms, vascular plant detritus, mineral particles, and amorphous detritus using a Whipple grid. We counted and identified material observed at grid intersections. We counted at least 50 intersections per sample from *Glossosoma* guts and at least 150 intersections per sample from heptageniid guts. Algal cells were rarer in heptageniid guts, so we needed a larger sample to reliably determine the percentage of algae.

Watershed survey

To examine carbon sources used by primary consumers in riffle habitats within the surrounding South Fork Eel River watershed, we analyzed stable carbon isotope ratios of grazing caddisflies (*Glossosoma penitum*, *Glossosoma califica*, and *Neophylax rickeri*) and heptageniid mayflies (*Cinygma*, *Cinygmula*, *Nixe*, and *Epeorus* spp.) from 10 streams with drainage areas ranging from 0.8 to 140 km^2. These streams encompass a gradient in algal productivity ranging from extremely low levels, in the smallest headwater streams, to highly productive rivers (Finlay 2004, McNeely 2004). Description of the streams' physical habitat can be found in Finlay (2003, 2004). The insects were sampled during July and August of 1998 and 1999. We removed insects' guts and dried the insects at 50°C for 48 hours. We combined 3–30 insects from each taxon at each site on each of the sampling dates to form composite samples. We determined stable carbon isotope ratios on a Europa 20-20 continuous flow mass spectrometer at the University of California Berkeley Center for Stable Isotope Biogeochemistry.

RESULTS

We found high densities of *Glossosoma* larvae in Fox Creek through the summer. The removal achieved a 70% reduction in the number of *Glossosoma* and an 80–90% reduction in estimated biomass, compared with control plots (Table 1). *Glossosoma* made up 25% ± 6.9% (mean ± SE) of invertebrate biomass in benthic samples in June (premanipulation, all plots, $N = 10$), 53.3% ± 3.4% in August (controls, $N = 5$), and 17.7% ± 7.0% in

September (controls, $N = 5$; Fig. 1). There was no difference in mean chlorophyll *a* per area between experimental and control plots in early June before the manipulations were established. Algal biomass (measured as chlorophyll *a*) approximately doubled in response to reduction in *Glossosoma* densities in August and September (Table 1).

In early June, before the manipulation, and in August, after one month of manipulation, there were no significant differences between treatments in biomass of invertebrates other than *Glossosoma*. By September, the previously defined guild of vulnerable primary consumers had significantly higher biomass in removal plots than in control plots (Table 1). Within this guild, there was a marginally significant increase in heptageniid mayfly biomass in removal plots. There was no difference in biomass of Chironomidae between treatments (Table 1). There were marginally significant trends toward higher biomass of invertebrate predators and perlid stonefly larvae in removal plots (Table 1). These trends appear particularly dramatic because they reversed an initially higher biomass of predators in control plots prior to the manipulations (Table 1). This June difference was the result of a few very large stoneflies (>20 mg) in control plots and was likely due to chance. Animals in this cohort likely emerged before the August sampling. Although the magnitude of the trend for higher predator biomass in removals was large (more than three times the biomass of predators in removals as controls, and more than seven times the biomass of perlid stoneflies in removals as controls), we had low statistical power to detect it due to the low density of large stoneflies, which produced high variability in biomass.

There were seasonal shifts in the stable carbon isotope ratios in stream grazers, indicating changes over time in the proportion of carbon they assimilated from algae. In June samples, heptageniids had carbon isotope ratios relatively depleted in ^{13}C, indicating significant reliance on algae, although carbon isotope ratios for heptageniids were less depleted in ^{13}C than for *Glossosoma*
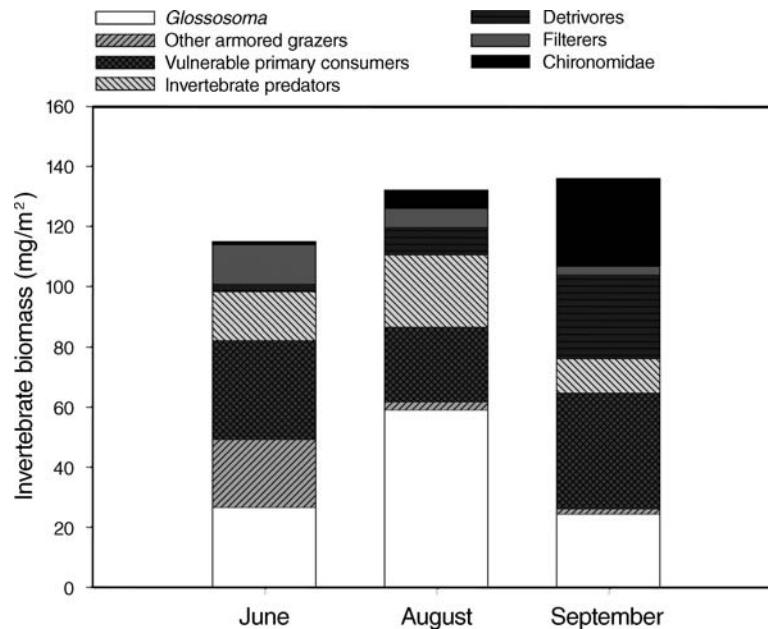
Fig. 1. Relative biomass of invertebrate guilds collected from Fox Creek (California, USA) benthic stone samples. June data are all invertebrates collected from 60 cobbles in 10 experimental plots (premanipulation, 6 cobbles/plot). August and September data are all invertebrates collected from 30 cobbles in five plots (control plots only, 6 cobbles/plot).

(Table 2). By August, heptageniid carbon isotope ratios increased, indicating more assimilation of terrestrial carbon. Mixing models suggested that June mayfly tissue contained 28–63% algal carbon and that control mayfly tissue in September contained 3–24%. (The lower value for each month is the low end of 95% CI, assuming 50% *Glossosoma* carbon was algal, while the higher value is the high end of 95% CI, assuming 100% *Glossosoma* carbon was algal. We used this method to construct all ranges presented.) In contrast to the mayflies, *Glossosoma* $\delta^{13}C$ decreased over time, tracking seasonal decreases in algal $\delta^{13}C$ caused by increasing stream water CO_2 concentrations (Finlay 2004), consistent with their primary reliance on algal carbon. Mixing models suggested that psphenid beetle larvae sampled in September obtained 13–51% of their carbon from algae. Perlids obtained their carbon from prey that relied on terrestrial sources throughout the summer. Although

perlid $\delta^{13}C$ was higher than that of terrestrial detritus collected during the experiment, it was within the range of detritivores (shredders) collected from this stream and was consistent with a small trophic fraction of $\delta^{13}C$ with trophic transfer of C (Fry and Sherr 1984, Finlay et al. 1999; J. C. Finlay, *unpublished data*).

Isotope analyses also suggested that *Glossosoma* removal shifted the diets of vulnerable heptageniid mayflies. There were no significant differences between controls and removals in $\delta^{13}C$ of any taxon prior to initiating the removals (Table 2). In September, stable carbon isotope ratios of heptageniid larvae from removal plots were slightly but significantly more negative than ratios of larvae from control plots (Table 2), suggesting that the mayflies consumed more algae when *Glossosoma* were removed. The mixing models suggested that mayfly tissue from control plots sampled in September contained 3–24% algal carbon and that

TABLE 2. Stable carbon isotope ratios ($\delta^{13}C$) of consumers and detritus from Fox Creek, California, USA, in summer 2000.

	June		August		September			
Guild	Control	Removal	Control	Removal	Control	Removal	t	P
Glossosoma	−35.51 (0.34)		−35.91 (0.85)		−36.89 (0.86)			
Heptageniidae	−32.67 (0.63)	−32.72 (0.89)	−30.28 (0.43)	−30.62 (0.52)	−30.39 (0.52)	−31.37 (0.82)	−2.599	0.032
Perlidae	−28.66 (0.49)	−28.49 (0.39)	−27.11 (0.30)	−28.04 (0.54)	−27.32 (0.42)	−27.60 (0.18)	−1.126	0.162
Psphenidae					−32.16 (0.75)	−32.85 (1.07)	−1.144	0.158
Terrestrial detritus	−28.50 (0.20)	−28.00 (0.33)	−28.72 (0.17)	−29.19 (0.26)	−29.25 (0.21)	−29.05 (0.19)	−1.035	0.821

Notes: Stable carbon isotope values (means with SE in parentheses) of epilithic algae should be similar to or slightly more negative than those of *Glossosoma* larvae. Values of five paired control and *Glossosoma* removal plots were compared using a one-tailed *t* test. There were no significant differences in June (premanipulation) or August (30 days after manipulation). In September (60 days after manipulation), heptageniid mayflies had significantly lower $\delta^{13}C$ in removal plots, suggesting that they may have been feeding on epilithic algae more in these plots.
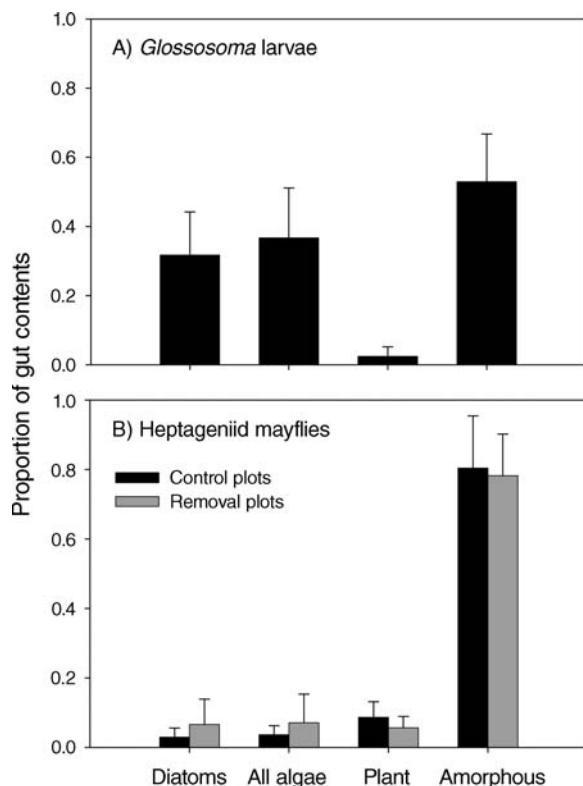
FIG. 2. Gut contents of (A) *Glossosoma* larvae and (B) heptageniid mayfly larvae from experimental plots, September 2000. Data are means with standard error. Recognizable algae made up 35% of *Glossosoma* gut material but only 3.7% of the heptageniid gut material in control plots. Guts of heptageniids from *Glossosoma* removal plots contained twice as much algae as those from control plots (paired one-tailed t test on transformed (arcsine square-root) proportions, $N = 4$, $t = -3.029$, $P = 0.028$). The sample size is reduced from 5 to 4 for Heptageniidae because one sample was lost.

mayfly tissue from removal plots contained 7–42% algal carbon. We did not observe a significant response to *Glossosoma* removal in the $\delta^{13}C$ of perlid stoneflies or of heptageniids in August.

Analyses of gut contents were consistent with stable isotope results. We analyzed the gut contents of heptageniid mayflies and *Glossosoma* collected during September. In all plots, amorphous detritus of unidentifiable origin made up most of the material in heptageniid guts. However, heptageniid larvae from *Glossosoma* removal plots had a higher proportion of recognizable diatoms and algal cells in their guts than those from control plots (Fig. 2). Algal cells constituted 19–56% of the material in larval *Glossosoma* guts.

Surveys of streams across an algal productivity gradient showed that heptageniid mayflies sampled from the South Fork Eel River watershed had $\delta^{13}C$ ranging from −33 to −23 (Fig. 3). For grazing caddisflies, $\delta^{13}C$ ranged from −44 to −23. Heptageniid mayfly stable carbon isotope ratios were intermediate between those of detritus and those of grazing caddisflies and expected

for algae in small unproductive streams (drainage area <10 km²). Heptageniid mayfly stable carbon isotope ratios converged to ratios similar to grazing caddisflies and algae in larger, more productive streams (Fig. 3).

DISCUSSION

In-stream production of algae provides substantial carbon and energy to primary consumers in Fox Creek, despite its headwater landscape position, dark forest canopy, and low algal standing crops and productivity. Caddisflies that feed primarily on algae made up 40–50% of benthic invertebrate biomass through much of the summer. Heptageniid mayflies and psphenid beetle larvae also assimilate some algal carbon. These animals made up an additional 15–25% of invertebrate biomass. In contrast, predators derive most of their carbon from prey feeding on terrestrial plants or terrestrial plant detritus.

Our data were collected in summer, and the relative importance of algae and detritus as carbon sources may vary seasonally. Although algal carbon may be less important in other seasons, summer is a crucial period of growth for stream organisms in the mediterranean climate of northern California (Gasith and Resh 1999). Grazing *Glossosoma* or *Neophylax* caddisfly larvae are present and very abundant throughout the year.
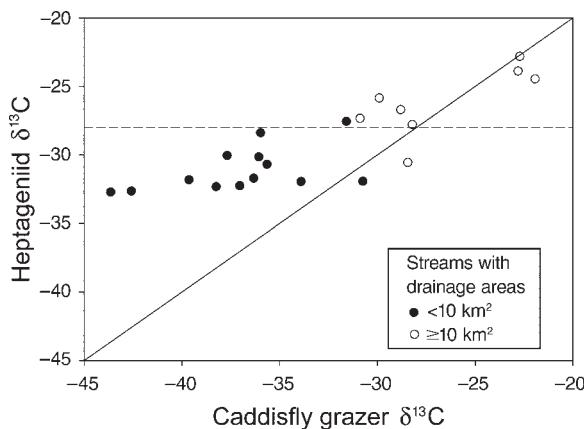

FIG. 3. Stable carbon isotope ratios of heptageniid mayfly larvae (*Cinygma, Cinygmula, Nixe,* and *Epeorus*) from the South Fork Eel River watershed (California, USA) plotted against those of grazing caddisflies (*Glossosoma penitum, Glossosoma califica,* and *Neophylax rickeri*). Each point represents isotope ratios of caddisflies and mayflies collected from the same stream and habitat on the same date. Streams range from drainage areas of 0.8 to 145 km². Algal $\delta^{13}C$ values generally increase with stream size in the watershed (Finlay 2004); the most ^{13}C-depleted values correspond to the smallest and least productive streams. Solid circles represent streams with drainage areas <10 km². Open circles represent streams with drainage areas ≥10 km². In small unproductive streams, mayflies' carbon isotope ratios are intermediate between those of detritus (dotted line) and scraping caddisflies. As stream size increases, the stable carbon isotope ratios of mayflies and caddisflies converge.

Although inputs of coarse terrestrial detritus are highest in autumn, they are flushed relatively quickly by high stream flows in late fall (C. McNeely, *unpublished data*). These observations suggest that the relative importance of algae to stream consumers in other seasons may be similar to its importance in summer.

Removal of the dominant grazer (*Glossosoma*) affected biomass of other invertebrates and, to some extent, the energy sources of an abundant primary consumer. Given the modest spatial and temporal scale of the experiment, biomass increases were probably due to behavioral choices of invertebrates to colonize and remain in removal plots and possibly to faster growth of animals in removal plots. The duration of the experiment was too short for reproductive recruitment of many species (Butler 1984), and emerging adults would have likely dispersed widely before laying eggs (Hershey et al. 1993, Peckarsky et al. 2000).

Effects of *Glossosoma* larvae on behavior of other invertebrates may arise through several mechanisms. First, some primary consumers compete with *Glossosoma* for algal food. We observed changes in heptageniid mayfly diet following *Glossosoma* removal that suggest greater consumption of algae in response to release from competition. Although heptageniid diets clearly shifted, the increase in algal carbon was modest. Stable carbon isotope ratios suggest a higher contribution of algae to heptageniid carbon than does the proportion of algal cells found in their guts. Material categorized as "amorphous detritus" may include algal fragments and exudates (Lock et al. 1984). Assimilation rates of algae are higher than those of detritus for many taxa (Benke and Wallace 1980, Slansky and Schriber 1982), perhaps as a consequence of algae having more proteins and lipids, and less cellulose or lignins, than terrestrial detritus (Boyd 1973, Lamberti 1996).

Mayflies appeared to use substantial terrestrial carbon even when released from competition with *Glossosoma*, and shifts in diet and isotope ratios were smaller than we expected. The relatively small responses of heptageniids to the *Glossosoma* removal is likely due to the high drainage network position of the experimental sites. In these small, unproductive headwaters, we may have been near the upstream edge of the longitudinal productivity gradient at which food web consequences of *Glossosoma* removal could be detected with such an experimental manipulation. Heptageniid mayflies in the South Fork Eel River watershed consume algal and detrital carbon in proportion to their abundance within epilithic biofilms (McNeely et al., *in press*). In contrast to the mayflies, *Glossosoma* selectively feed on algae (McNeely et al., *in press*); this selective feeding may deplete biofilms of algae, reducing their availability to the mayflies. Unmanipulated biofilms in Fox Creek contain primarily allochthonous carbon (McNeely et al., *in press*), and biofilms may be primarily allochthonous even when *Glossosoma* grazing is reduced. Caddisfly activity and feeding may cause sloughing of biofilms,

reducing the total amount of food (algal and detrital) available to the mayflies (Steinman 1996, Kuhara et al. 2000).

Competition between caddisflies and mayflies may be widespread in unproductive streams. Patterns of primary consumer–stable carbon isotope ratios in the South Fork Eel River watershed show that heptageniids include algae in their diet in small tributaries, but that caddisflies use substantially more algal carbon in those streams (Fig. 3). Stable isotope ratios of algae are predicted to increase with stream size in the South Fork Eel River watershed, and grazing caddisfly $\delta^{13}C$ tracks the $\delta^{13}C$ expected for algae along this gradient (Finlay 2004). As stream size and productivity increase, $\delta^{13}C$ of the two groups becomes similar, suggesting that competition with caddisflies for algae does not constrain mayfly diet in productive streams, and that both groups assimilate primarily algal carbon in productive streams. Competition between glossosomatid caddisflies and mayflies has also been demonstrated in unproductive streams in northern Japan (Kuhara et al. 1999, 2000), although carbon sources used by the insects were not determined.

Glossosoma larvae may interact with stream invertebrates through other mechanisms in addition to competition. Our data suggest links between algivores and the detrital food web in Fox Creek. Biomass of vulnerable primary consumers increased where *Glossosoma* were removed, and many of these species are supported primarily by terrestrial carbon (Finlay 2001; Finlay, *unpublished data*). These effects are likely due to physical interference by *Glossosoma* larvae (i.e., "bulldozing") as has been shown for other grazers (Dayton 1971, Wootton et al. 1996, Hannaford 1998). *Glossosoma* movements may also disturb and export detrital organic matter (Steinman 1996). There was also a marginally significant trend for increased predator biomass where *Glossosoma* densities were reduced, but there was no evidence for an effect on predator carbon sources, suggesting that predator densities may be affected through the detrital food web. However, the duration of the experiment may not have been long enough for changes in primary consumer $\delta^{13}C$ to cause measurable changes in stonefly predators. Invertebrate movement into plots might also have masked local responses to increased algal availability within removal plots.

Grazers such as caddisflies and snails are known to be important components of stream communities; they can strongly limit algal biomass and the success of other primary consumers (McAuliffe 1984, Feminella and Resh 1991, Kohler 1992, Steinman 1992, Rosemond et al. 1993). Although these effects are well known in more productive streams (Feminella and Hawkins 1995, Steinman 1996), forested headwaters have traditionally been considered donor-controlled (sensu Pimm 1982) communities supported by terrestrial inputs (Minshall 1967, Vannote et al. 1980, Wallace et al. 1997). Our data

suggest that algivorous caddisflies play an important role in headwater streams. The community structure we observed, where competitively dominant predator-resistant grazers make up a substantial portion of the stream biota but where much of the community is supported by detrital inputs, may not be unusual in headwater streams (e.g., Newbold et al. 1983, Mayer and Likens 1987). Although algae contribute a small portion of the organic-matter budget in unproductive headwaters, they can support a disproportionately large proportion of the consumer biomass and secondary production (Coffman et al. 1971, McCutchan and Lewis 2002). In addition, our data suggest that interactions with algivorous caddisflies affect the biomass of invertebrates that consume little algae. If detrital and algal food webs are linked by species interactions such as interference or exploitative competition, grazers and algae may have important effects on populations of detritivores and predators in headwater streams and may influence flows of terrestrial carbon.

Competition from armored grazers increases the reliance of a predator-vulnerable primary consumer on terrestrial inputs. Although we did not observe shifts in carbon sources to higher trophic levels in our manipulations, competition among primary consumers with different vulnerabilities to predation could have such an effect in streams where both terrestrial detritus and algae are available. Such effects might be stronger in streams with higher productivity than our study site or where armored primary consumers are even more dominant (e.g., streams with 95% of invertebrate biomass in snails). Studies that combine investigations of energy flow with manipulative experiments (e.g., Nakano et al. 1999, Nakano and Murakami 2001, Sabo and Power 2002) should improve our understanding of how species interactions influence stream communities' links to the watersheds that surround them.

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APPENDIX

Macroinvertebrate guild assignments and length–biomass regressions (*Ecological Archives* E088-024-A1).