

SPATIAL VARIATION IN CADDISFLY GRAZING REGIMES WITHIN A NORTHERN CALIFORNIA WATERSHED

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Abstract. Ecologists seek better understanding of why species interactions change across space and time in natural communities. In streams, species effects on resources and community structure may change as physical characteristics of the stream environment change along drainage networks. We examined spatial and seasonal effects of armored grazers using a small-scale exclusion experiment that was replicated in streams of different drainage areas. Effects of grazing varied with stream size and were related to variation in grazer abundance and phenology. We identified three distinct grazing regimes and a stream size (drainage area [DA]) threshold corresponding to a shift from one to two functional trophic levels. In streams with DA < 1 km², armored grazers did not reduce biomass of algal biofilms. In slightly larger streams (2–3 km² DA), the armored grazer guild was dominated by bivoltine *Glossosoma*. These caddisflies persisted and limited algal biofilms throughout the summer in one of these streams. In the largest tributaries (DA > 10 km²), the grazer guild was dominated by univoltine caddisflies, and grazing limited algal biofilms in early summer, but not late summer, after caddisflies pupated. Drainage area is a useful predictor of spatial transitions in food web interactions within and among watersheds. Quantifying the drainage area threshold at which interactions change in catchments with differing geology, vegetation, hydrology, climate, land use, or species pools should help build the understanding we need to forecast ecological responses to environmental change.

Key words: Angelo Coast Range Reserve, California, USA; armored grazer; caddisfly; landscape; phenology; threshold; trophic level; watershed.

INTRODUCTION

Ecologists would like to predict when and where species will have strong impacts on natural communities. Landscape position may serve as one such predictor (Naiman and Sedell 1980, Vannote et al. 1980, Menge et al. 1994, Kratz et al. 1997, Power and Dietrich 2002, Woodward and Hildrew 2002, Seastedt et al. 2004). Within areas of similar geology and rainfall, physical structure of stream habitats varies systematically with increasing drainage area (Leopold et al. 1964, Montgomery and Buffington 1993). These changes in stream habitat can affect organisms directly (Poff 1997, Wiley et al. 1997) and may also affect their interactions (Power and Dietrich 2002, Woodward and Hildrew 2002). Physical and chemical traits of lake, alpine, and rocky intertidal environments also vary systematically with landscape position and water flow paths in ways likely to affect community interactions (Menge et al. 1994, 2004, Kratz et al. 1997, Seastedt et al. 2004). The effects of physical habitat on aquatic organisms have generally

been studied at small scales, and controls may often operate at these scales (Wiley et al. 1997). By predicting small-scale habitat traits, drainage area and landscape position within watersheds may predict the strength and outcome of community interactions over relatively large spatial scales compared to the scales at which these interactions occur. We selected a common and ecologically important stream food web interaction, grazing on benthic algae by armored insect grazers, and investigated how its strength varied with drainage area in the South Fork Eel River watershed in northern California, USA.

Insect grazers limit algal growth in many but not all streams (Lamberti and Resh 1983, McAuliffe 1984, Feminella et al. 1989, Feminella and Hawkins 1995, Lamberti 1996, Kohler and Wiley 1997, Peterson et al. 2001). Several studies have shown variation in the strength of insect control of algae as a result of variability in primary productivity (Feminella et al. 1989, Lamberti et al. 1989, Feminella and Hawkins 1995), disturbance (Feminella and Resh 1990, Power 1992a, Power et al. 1996), flow velocity (Hart 1992, Poff and Ward 1995), and substrate type and heterogeneity (Kjeldsen et al. 1996, Robson 1996). Water temperature may also affect grazing through effects on consumer species composition (Hawkins et al. 1997) and insect phenology (MacKay 1979, Butler 1984, Hannaford

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1998). These factors all vary systematically with drainage area within forested watersheds (Leopold et al. 1964, Brown 1969, Hynes 1970, Vannote et al. 1980, Montgomery and Buffington 1993, Lamberti and Steinman 1997), suggesting that they may generate predictable patterns in grazer effects within watersheds.

We examined the manner in which effects of the armored grazer guild, which has an important role in stream food webs, vary with drainage area in a watershed. Armored grazers feed on algae, but are protected from predators by a stone case or shell. They can be more effective in reducing algal biomass than other grazers such as mayflies (Kohler 1992, Feminella and Hawkins 1995). If these animals compete with more vulnerable grazers, they may reduce or prevent transfer of energy fixed by algae to predators (Tait et al. 1994, Power 1995). They may influence both energy flow pathways in streams (Power et al. 1996, Power and Dietrich 2002) and the ability of predators to exert top-down control of their prey (Lamberti 1996, Power et al. 1996).

We developed two a priori hypotheses about the manner in which armored grazer effects would vary among tributaries in a northern California watershed. In shaded, unproductive headwaters, we expected that the strength of grazing by armored insects would increase with stream size, light availability, and primary productivity. In many forested watersheds, increasing light availability with drainage area leads to increasing primary productivity (Minshall 1978, Naiman and Sedell 1980, Vannote et al. 1980, Lamberti and Steinman 1997). With downstream increases in primary productivity, food chain theory (Fretwell 1977, Oksanen et al. 1981) predicts a shift from communities in which plants are primarily limited by their resources (one functional trophic level) to communities in which they are primarily limited by herbivores (two functional trophic levels). Trophic levels are considered "functional" if they can reduce the standing crops of resources at the next lower trophic level (Fretwell 1977). Their impact, whether direct or indirect, substantially alters the biomass of plants, algae, or other basal resources through an entire system, via "community-level cascades" (Polis et al. 2000). Grazer effects in artificial streams increased with algal productivity (Lamberti et al. 1989). We hypothesized that as primary productivity increases along drainage area gradients in the South Fork Eel River watershed, the strength of grazing by armored grazers would increase, and food chains should lengthen from one to two functional trophic levels. Alternatively, if algal productivity increased faster than grazing rates, grazer control over algae might weaken downstream.

We also hypothesized that variation in grazer phenology might affect grazing regimes within the watershed. Phenology of planktonic and littoral grazers is important to seasonal succession and spatial variation in algal growth in lakes (Lampert 1978, Sommer et al. 1986, Harrison and Hildrew 2001). Variation in species

composition of the armored grazer guild and environmental effects on grazer development rates could both lead to variation in armored grazer phenology. Taxa such as snails and multivoltine insects may be continuously present and active throughout the year, while univoltine species may be active only until the year's larval cohort pupates. Insect development accelerates with temperature (MacKay 1979, Butler 1984), and water temperature generally increases with stream width (Brown 1969, Hynes 1970), so armored grazing insects may develop more rapidly in larger, warmer streams. For univoltine species, faster development may lead to earlier pupation, leaving a longer period when larvae of the species are not active in the stream (Hannaford 1998). We hypothesized that algae might be released from grazing earlier in larger, warmer streams and grazing might remain important through more of the growing season in smaller, cooler streams. However, this pattern might be altered by changes in species composition of the armored grazer guild (Hawkins et al. 1997), particularly shifts between multivoltine and univoltine species.

We tested our hypotheses with grazer exclusion experiments in seven stream sites of varying drainage area in the South Fork Eel River drainage, Mendocino County, California (Fig. 1). We also monitored armored grazer populations and estimated primary productivity to test mechanisms driving spatial and temporal variation in grazing.

METHODS

Study site

We surveyed six tributaries of the South Fork Eel River within or near the University of California's Angelo Coast Range Reserve (Mendocino County; Fig. 1, Table 1). The regional climate is Mediterranean, with cool, rainy winters and warm, dry summers. High winter flows scour algae from the streams, which recover after discharge drops and the water clears in the late spring (Power 1992a). All six streams flow into the South Fork Eel River within or near the University of California's Angelo Coast Range Reserve. The watershed is steep and covered with mixed conifer hardwood forest dominated by Douglas fir (*Pseudotsuga menziesii*). The streams range in drainage area (DA) from 0.5 to 17 km². One of the streams (Elder Creek) was studied at two sites: close to its confluence with the South Fork Eel River (DA = 17 km²) and ~2 km upstream (DA = 13.5 km²). Within the watershed, canopy cover declines and light availability, primary productivity, and water temperature increase with drainage area (Table 1; Finlay 2004). Armored grazer populations are dominated by stone-cased caddisflies. Grazers vulnerable to predators include mayfly larvae (Ephemeroptera: Heptageniidae and Baetidae), beetle larvae (Coleoptera: Psephenidae), and midges (Diptera: Chironomidae) (McNeely et al. 2007). In many of the study streams, however, vulnerable grazers consume primarily non-algal components of

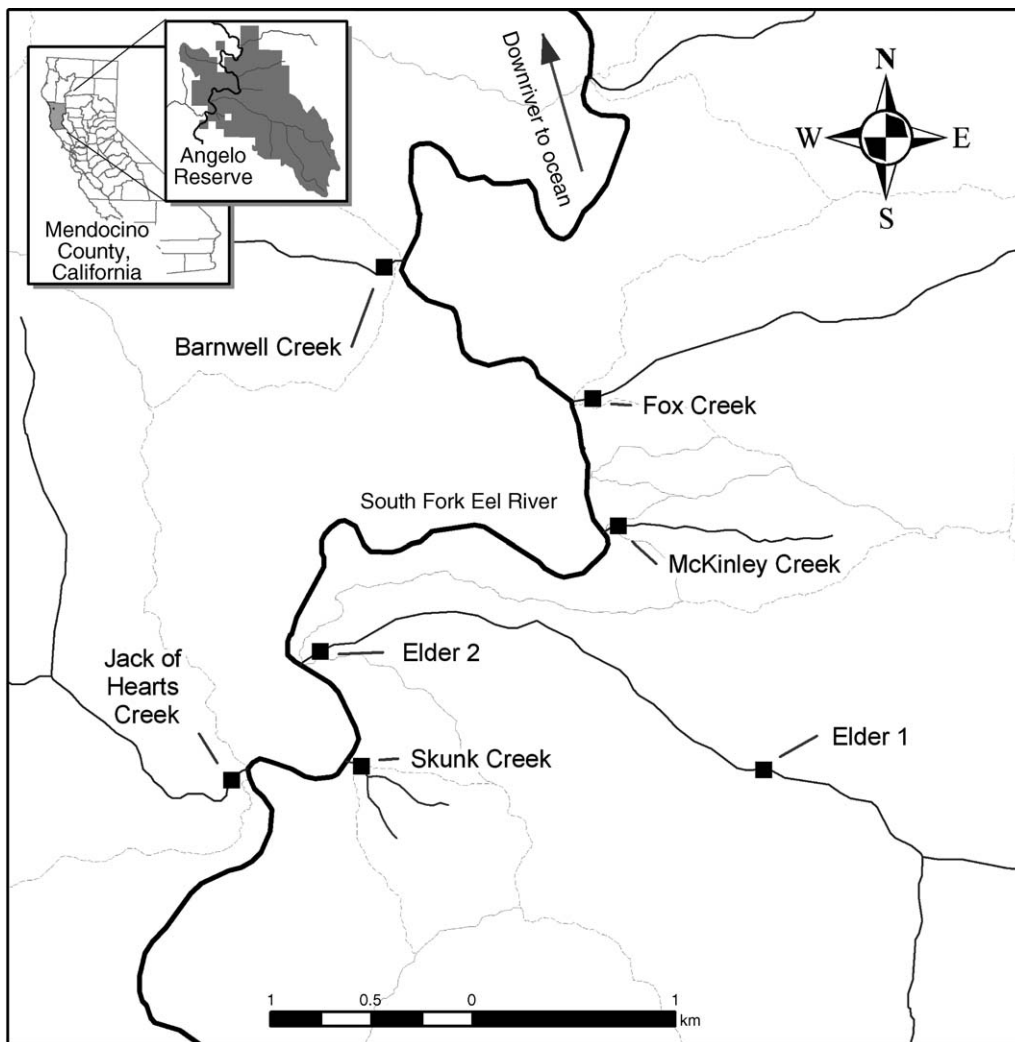


FIG. 1. Map of the South Fork Eel River watershed in California, USA, showing study sites.

TABLE 1. Summary of physical characteristics of stream sites, dominant armored grazer species, and effects of armored grazers on tile biofilms.

Stream site	Drainage area (km ²)	Width (m)	Percent cover	Temperature (°C)	Early summer				Late summer			
					Dominant grazer	Grazing effects		Dominant grazer	Grazing effects			
						AFDM	Chlor. <i>a</i>		AFDM	Chlor. <i>a</i>		
Skunk	0.55	0.37 ± 0.12	97	13	<i>G. penitum</i>	(-5%)	(+13%)	<i>G. penitum</i>	(-30%)	(-17%)		
McKinley	0.59	0.56 ± 0.12	93	13.5	<i>G. penitum</i> , <i>N. rickeri</i>	(-12%)	(-15%)	<i>G. penitum</i>	(+22%)	(+3%)		
Barnwell	2.0	1.06 ± 0.34	93	15	<i>G. penitum</i> , <i>N. rickeri</i>	-68%	-69%	<i>G. penitum</i>	(+0.7%)	(+40%)		
Fox	2.8	1.39 ± 0.15	95	14	<i>G. penitum</i>	-39%	(-23%)	<i>G. penitum</i>	-55%	-45%		
Jack of Hearts	9.9	2.47 ± 0.32	81	18	<i>D. gilvipes</i>	-50%	-40%	very few (<i>G. califica</i> , <i>D. gilvipes</i>)	(+0.2%)	+125%		
Elder 1	13.5	3.95 ± 0.85	80	15	<i>D. gilvipes</i>	-35%	(+10%)	<i>G. califica</i>	(-29%)	(-7%)		
Elder 2	16.9	4.12 ± 0.39	78	18	<i>D. gilvipes</i>	-38%	(-18%)	<i>G. califica</i>	(-12%)	(-18%)		

Notes: Abbreviations: genera are: *G.*, *Glossosoma*; *N.*, *Neophylax*; and *D.*, *Dicosmoecus*; Chlor. *a* is chlorophyll *a*. Widths are means ± SE of July 2001 caddisfly census transects. Percent cover was determined by a spherical densiometer along four transects/site. Temperatures were opportunistically measured with an alcohol thermometer, midday during July 2001. Effects are reported as percentage of difference in grazed and ungrazed tiles relative to abundances on ungrazed tiles. If the difference is not significant, it is reported in parentheses. "AFDM" is ash-free dry mass.

biofilms (Finlay 2001, McNeely et al. 2006). Juvenile steelhead (*Onchorhynchus mykiss*) are present in all but two ($DA < 1 \text{ km}^2$) of the study streams. In the smaller streams ($DA < 5 \text{ km}^2$), juvenile Pacific giant salamanders (*Dicamptodon tenebrosus*) are also abundant predators. Algae in these streams are primarily adnate diatoms and small clumps of blue-green algae (C. McNeely, *personal observation*).

Grazer exclusion

We placed unglazed ceramic tiles ($7 \times 14 \text{ cm}$) in each of seven stream sites to provide uniform sampling substrates for colonizing algae and bacteria. We harvested biofilms (tightly adhering organic film containing algal and bacterial cells) from the tiles in mid- and late summer. We placed 60 tiles in each site in early June 2001. Half of the tiles (30) were protected from armored grazers, half were exposed. We collected half of each treatment (grazer exclusion and control) in early July (midsummer, after 25 d of growth) and the other half in August (late summer, after 60 d of growth). Tiles that were turned over were excluded.

We used petroleum jelly to protect exclusion tiles from armored grazers. In streams with abundant *Dicosmoecus* larvae (Fig. 2B), we built small platforms (20 cm tall) by stacking two bricks (Table 1). We wrapped the bricks in plastic film and coated the film with petroleum jelly. On top of the bricks we placed a piece of linoleum ($18 \times 9.5 \text{ cm}$) and a small clay tile ($15 \times 7.5 \text{ cm}$). A 1-cm strip around the edge of the linoleum was coated with petroleum jelly, and the tile was placed within this margin. In streams ($DA < 3 \text{ km}^2$) in which *Dicosmoecus* larvae were rare (Fig. 2B), we placed the piece of linoleum with a petroleum jelly barrier directly on the stream bottom and the tile on top of the linoleum (Table 1). It was not possible to use the brick platforms in these streams because the water was too shallow. The linoleum-only design did not effectively discourage *Dicosmoecus* grazing, as *Dicosmoecus* larvae would tumble through the water column over this barrier, but did exclude smaller armored grazers that were abundant in the small streams (caddisflies *Neophylax rickeri* and *Glossosoma penitum*). *Dicosmoecus* were rare or absent in streams too shallow for brick platforms. Control tiles were placed on the streambed where they were accessible to grazers. We did not use bricks or linoleum without petroleum jelly in the controls, as these may have reduced grazing by armored grazers below ambient levels in the streams. Similar designs have been successful in excluding armored grazers with heavy cases, but they allow more mobile insects access (Lamberti and Resh 1983, McAuliffe 1984, Power 1984, Kuhara et al. 2000). We placed tiles in a specified flow range (6–10 cm/s, measured 3 cm above tile with a Marsh-McBirney Flowmate 2000; Marsh-McBirney, Frederick, Maryland, USA) to prevent flow differences between controls and exclusions. This flow range was common in all study streams. To sample tiles, we

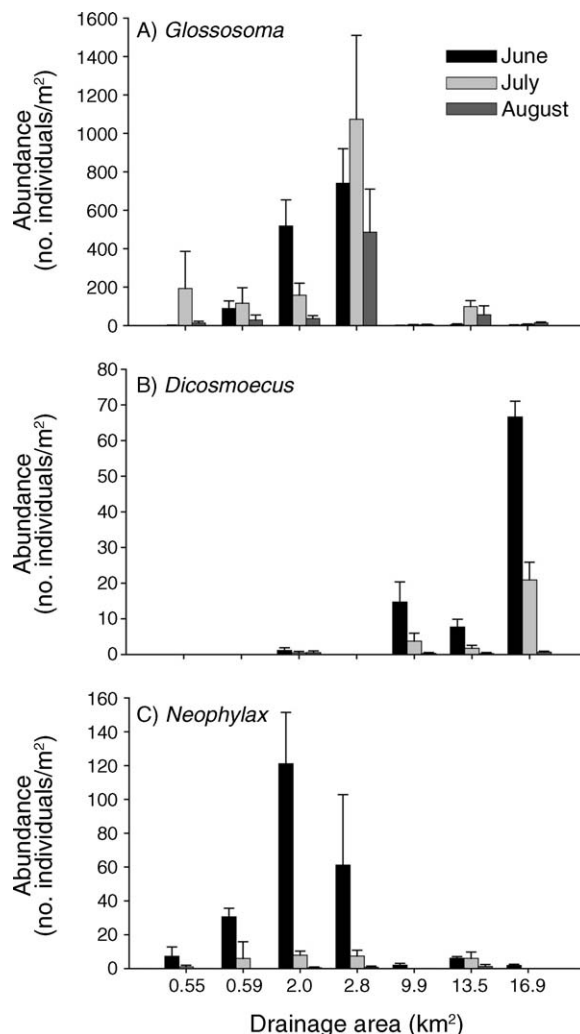


FIG. 2. Abundance (mean + SE) of (A) *Glossosoma* (*penitum* and *califica*), (B) *Dicosmoecus*, and (C) *Neophylax* larvae by drainage area in streams of the South Fork Eel River watershed in the summer of 2001.

removed biofilms with a wire brush. We used material from one-third of each tile (112.5 cm^2) to determine ash-free dry mass (AFDM) and material from one-third of each tile to determine chlorophyll *a* content. The remaining one-third was reserved for microscopic examination. Samples were kept cool and dark and filtered within 24 h. Chlorophyll *a* was measured by fluorometry (Steinman and Lamberti 1996).

To test grazing effects, we analyzed AFDM and chlorophyll *a* per area using ANOVA with site (random) and grazing treatment (fixed) as independent variables (Sokal and Rohlf 1995). The qualitative results were the same whether site was considered a random or fixed variable. We performed a separate ANOVA for each response variable on each sampling date. We log-transformed values to homogenize variances. To test grazing effects within streams, we compared trans-

formed AFDM and chlorophyll *a* values from grazed and protected tiles with orthogonal contrasts (Sokal and Rohlf 1995). The combined probability of a Type I error among all four ANOVAs was 0.19. All analyses were performed with JMP 4 (SAS Institute 2001). For mixed-model ANOVAs we used JMP to calculate mean squares and then computed *F* and *P* values according to Sokal and Rolf (1995) because JMP did not provide correct *F* values.

Caddisfly censuses

We censused sites to determine taxonomic composition, biomass, and life history status of the armored grazer guild three times: once before placing tiles in the streams (30 May–10 June), once after the first tile collection (20–25 July), and once after the final tile collection (22–27 August). We established five 0.5 m wide transects at each stream site. We counted the armored grazers present in these transects using a view box or mask and snorkel and measured the length of armored caddisfly cases with a ruler. To estimate biomass of the dominant armored grazer species (all caddisflies) without destructive sampling, we developed case length–body mass regressions (Appendix). To produce case–mass regressions, we collected larvae from areas near but at least 50 m away from the survey sites. We measured the length of the cases to the nearest millimeter with a ruler, killed the larvae by dipping them in hot water, and dried the animals for 48 h at 60°C, before weighing on a microbalance. For less abundant armored grazers (including snails and limpets) we collected individuals from near the study sites at the time of the census and used their mean dry mass as an estimate for individual biomass.

Primary productivity

We measured gross benthic primary productivity using a light-bottle/dark-bottle method (modified from Wetzel and Likens [2000], similar to methods of Fleituch [1999] and Fukuda et al. [2006]). We placed 20 7 × 7.5 cm clay tiles in the stream sites on 4–6 June 2002, in the same areas and flow conditions used for the grazing survey in 2001. We estimated primary productivity of tile biofilms between 23 July and 2 August 2002. We measured changes in oxygen concentration before and after incubating tiles in sealed glass jars (0.95 L) with local stream water in the dark and under ambient light and temperature conditions. At most sites we performed dark incubations in the morning (between 08:00 and 13:00 hours) for 3–5 h. At two sites with low standing crops of material, dark incubations were performed overnight (15 h). We performed light incubations in the early afternoon, between 12:00 and 15:00 hours for 0.25–3 h. At the beginning and end of each incubation period, we measured dissolved oxygen (DO) concentrations with a YSI model 550 meter (YSI, Yellow Springs, Ohio, USA). Sealed chambers can introduce artifacts into metabolism measurements, including increased

nutrient limitation, exclusion of hyporrhagic zones, and altered light and flow regimes (Vollenweider 1974, Bott et al. 1978, 1985, 1997, Uzarski et al. 2004). We used this method rather than whole-stream metabolism measurements (e.g., Marzolf et al. 1994) because we could isolate the habitat in which armored grazers were feeding and because it is difficult to estimate GPP with whole-stream methods in some highly heterotrophic study streams with high reaeration rates (C. McNeely, J. C. Finlay, M. Hondzo, M. E. Power, J. S. Schade, and S. Thomas, unpublished data). Although nutrient limitation and lack of flow in chambers may have reduced productivity below ambient levels, we used these measurements as a relative index of productivity among sites, which we expected to vary over a wide range.

RESULTS

Caddisfly abundance and phenology

Stone-cased caddisflies dominated the armored grazer guild in all of the study streams. In early summer, there was substantial armored grazer biomass (149–2162 mg/m²) at all but the smallest two stream sites (DA < 1 km²). Biomass of grazers increased with DA ($\log(\text{biomass, in milligrams}) = 1.659 + 1.087\log(\text{DA, in square kilometers})$; $r^2 = 0.82$, $P = 0.005$, $n = 7$). Dominant armored grazers included larvae of the caddisflies *Glossosoma penitum*, *Neophylax rickeri*, and *Dicosmoecus gilvipes* (Table 1). Other taxa contributed negligibly to the guild's total biomass. There was also consistent turnover in dominant species with stream size. In streams with drainage area < 3 km², *Glossosoma penitum* was the most abundant armored grazer in both numbers and biomass (Fig. 2A) and *Dicosmoecus* larvae were absent or rare (Fig. 2B). In larger streams, *Dicosmoecus* larvae were dominant (Fig. 2B). *Neophylax rickeri* was present throughout the gradient, but most abundant in small streams (DA = 2.0–2.8 km²; Fig. 2C). *Glossosoma califica* was found in larger streams (DA ≥ 10 km²; Fig. 2A).

The three dominant armored grazers differed in their phenology. Univoltine *Neophylax rickeri* and *Dicosmoecus gilvipes* densities declined markedly over the summer, both in numbers and biomass (Fig. 2B, C). In sites in which *Dicosmoecus* larvae were the dominant armored grazer, biomass of the guild dropped substantially over the summer (Fig. 3). In one site in which multivoltine *Glossosoma* larvae were dominant (Fox Creek, DA = 2.8 km²), armored grazer biomass did not drop substantially by the end of the summer (Fig. 3). At other sites dominated by *Glossosoma* (DA = 0.5–2 km²), caddisfly populations declined despite the continued presence of early instar larvae, resulting in declines in armored grazer biomass.

Primary productivity

Estimates of gross primary productivity increased with drainage area ($\log(\text{primary productivity}) = 1.433 + 0.560\log(\text{DA, in square kilometers})$; $r^2 = 0.76$, $P = 0.011$,

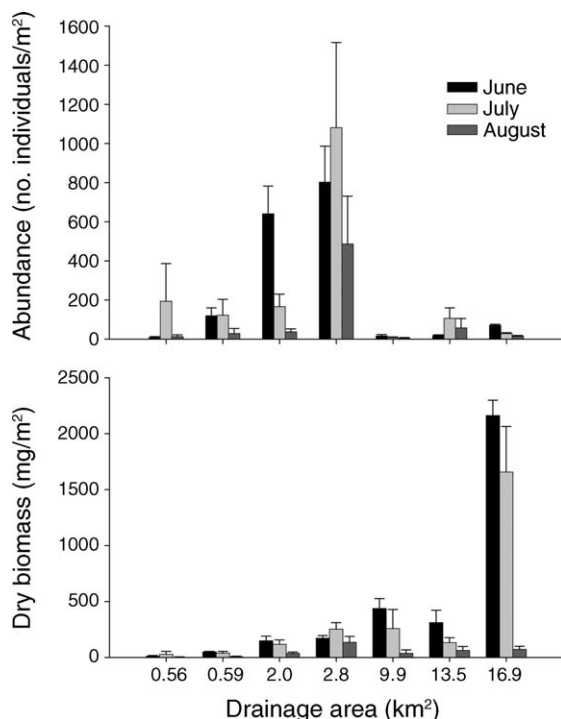


FIG. 3. (A) Abundance and (B) biomass (mean + SE) of armored grazers by drainage area in the South Fork Eel River watershed in the summer of 2001.

$n = 7$). Biomass of armored grazers tracked increasing primary productivity closely in early summer (June) but not late summer (August; Fig. 4).

Grazer exclusion

In midsummer (July) armored grazers reduced algal growth at most of the sites surveyed where drainage areas exceeded 1 km^2 (Fig. 5A). In midsummer, site, grazer treatment (exclusion or control), and the site \times treatment interaction significantly affected biomass on tiles (AFDM, Table 2). Within-site comparisons revealed that armored grazers significantly reduced biomass at four sites and marginally reduced biomass at a fifth site (all $\text{DA} > 1 \text{ km}^2$; Tables 1 and 2). At the two smallest sites ($\text{DA} < 1 \text{ km}^2$), grazing treatment did not affect biomass. Armored grazers affected chlorophyll a per area in fewer sites. In an ANOVA of log-transformed data, site and the site \times treatment interaction affected chlorophyll a per area. There was a significant difference between treatments at only two sites ($\text{DA} = 2.8$ and 9.9 km^2 ; Tables 1 and 2); grazers reduced AFDM at both of these sites as well. By late summer (August, 60 d of incubation), grazer effects on biomass were no longer detectable at most sites (Tables 1 and 3, Fig. 5C). Within-site comparisons revealed a significant reduction in biomass by grazers at only one site (Fox Creek, $\text{DA} = 2.8 \text{ km}^2$; Table 3, Fig. 5C). At one site (Jack of Hearts Creek, $\text{DA} = 9.9 \text{ km}^2$) there was

significantly more chlorophyll on grazed than on ungrazed tiles (Tables 1 and 3, Fig. 5D).

DISCUSSION

We identified two drainage area thresholds at which grazing regimes changed in the South Fork Eel River watershed. Grazing by armored grazers limited biomass of epilithic biofilms in streams with drainage area $> 1 \text{ km}^2$, but not smaller streams. Streams with drainage area $< 1 \text{ km}^2$ included in our study were the smallest permanently flowing streams in the area. Our observations suggest that these streams have only one functional trophic level (*sensu* Fretwell 1977, Oksanen et al. 1981) in the algal food chain, despite isotopic evidence that armored caddisflies there derive their carbon from algae (Finlay 2001, 2004, McNeely et al. 2006). Armored grazer biomass was low in very small headwater streams ($< 1 \text{ km}^2$), most individuals were small, and distributions were patchy. Such observations suggest that the lack of measurable grazing was not an artifact of the experimental methods. Although non-armored aquatic insects (e.g., mayfly nymphs and chironomid larvae) were not excluded by the manipulations, it is unlikely that they

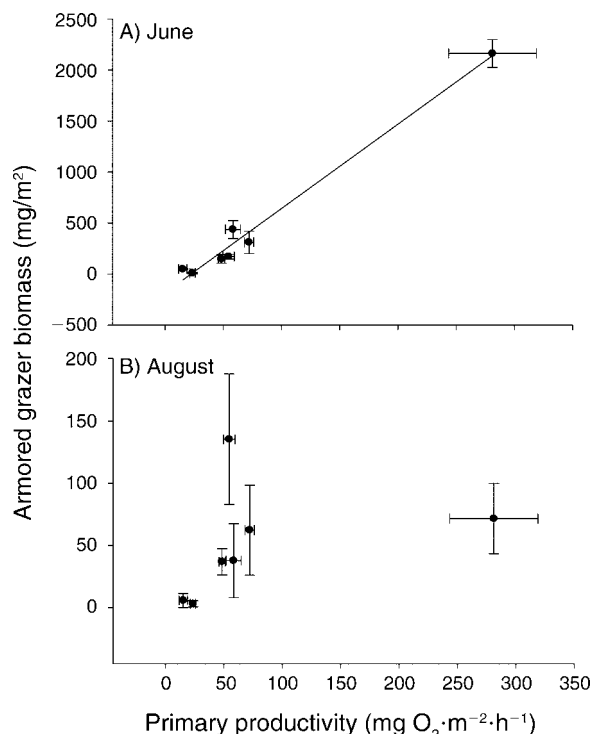


FIG. 4. Regressions of armored grazer biomass and primary productivity. (A) In June, there was a significant relationship between algal productivity and biomass (caddisfly biomass = $-183.64 + 8.268(\text{primary productivity})$, $r^2 = 0.987$, $P < 0.001$). With the high-productivity site removed, the relationship remained significant ($r^2 = 0.700$, $P = 0.0378$). (B) In August, caddisfly biomass was not correlated with site productivity, whether or not the high-productivity site was included in the analysis (all data, $r^2 = 0.11$, $P = 0.47$; high-productivity point excluded, $r^2 = 0.39$, $P = 0.19$).

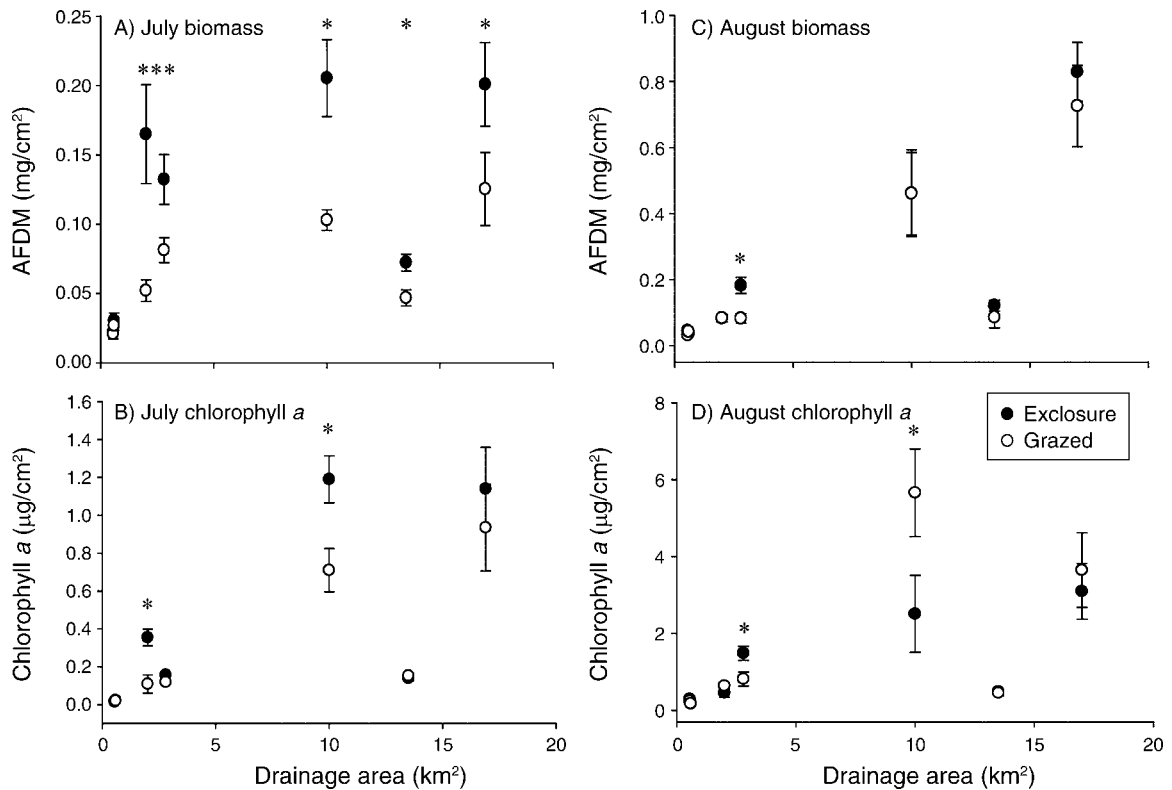


FIG. 5. (A) Biomass (AFDM, ash-free dry mass) and (B) chlorophyll *a* content in July, and (C) biomass and (D) chlorophyll *a* content in August of biofilms collected from exclusion tiles (no grazers) and control tiles (grazers). Data are means \pm SE. * $P < 0.05$; ** $P = 0.06$.

limited algae, as their isotopic signatures and gut contents indicated that they consume little algae in these unproductive tributaries (Finlay 2001, McNeely et al. 2006). In forested streams that drain $< 1 \text{ km}^2$, productivity may be too low to support enough herbivores to control algal biomass.

We observed strong effects of grazing in stream reaches with drainage area $> 1 \text{ km}^2$ in early summer. At this time, grazed tiles in larger streams had $< 65\%$ biomass of grazer-exclusion tiles. Biomass of armored grazers was correlated with the relative productivity of

tiles, suggesting that as a guild, they effectively track productivity of their food. In early summer algae and armored grazers may form a food chain with two functional trophic levels (sensu Fretwell 1977) in streams with DA $> 1 \text{ km}^2$. Streams with drainage areas of 2–3 km^2 in this watershed are particularly likely to fit the two-trophic-level scenario described by Fretwell (1977) and Oksanen et al. (1981). Armored grazers are largely ignored by local predators (Parker 1994, Wootton et al. 1996). Other, more vulnerable primary consumers in these streams depend largely on terrestrial primary

TABLE 2. Results of ANOVAs for ash-free dry mass (AFDM) and chlorophyll *a* collected from tiles incubated in different stream sites, with and without grazer exclusions, July and August 2001.

Source of variation	AFDM					Chlorophyll <i>a</i>				
	SS	df	MS	<i>F</i>	<i>P</i>	SS	df	MS	<i>F</i>	<i>P</i>
July 2001										
Site	16.632	6	2.773	55.90	< 0.0001	62.440	6	10.740	249.580	< 0.0001
Grazing	1.644	1	1.644	11.71	0.014	0.645	1	0.645	3.023	0.133
Site \times grazing	0.843	6	0.141	2.837	0.012	1.285	6	0.214	5.136	< 0.0001
Error	7.240	146	0.050			5.963	143	0.042		
August 2001										
Site	32.128	6	5.355	103.4	< 0.0001	31.246	6	5.208	70.280	< 0.0001
Grazing	0.341	1	0.341	2.583	0.159	0.014	1	0.014	0.052	0.827
Site \times grazing	0.800	6	1.334	2.58	0.021	1.631	6	0.272	3.669	0.002
Error	8.031	155	0.052			11.633	157	0.074		

TABLE 3. Results of ANOVA comparison of grazed and grazer-exclusion tiles at each site for ash-free dry mass (AFDM) and chlorophyll *a* in July and August 2001.

Site	AFDM						Chlorophyll <i>a</i>					
	DA (km ²)	SS	df	MS	<i>F</i>	<i>P</i>	DA (km ²)	SS	df	MS	<i>F</i>	<i>P</i>
July 2001												
Skunk	0.55	0.0007	1, 146	0.0007	0.013	0.908	0.55	0.008	1, 143	0.008	0.195	0.660
McKinley	0.59	0.008	1, 146	0.008	0.155	0.694	0.59	0.027	1, 143	0.027	0.651	0.412
Barnwell	2.0	1.267	1, 146	1.267	25.544	<0.0001	2.0	1.534	1, 143	1.534	36.792	<0.001
Fox	2.9	0.179	1, 146	0.179	3.600	0.060	2.8	0.100	1, 143	0.100	2.398	0.124
Jack of Hearts	9.9	0.396	1, 146	0.396	7.893	0.005	9.9	0.316	1, 143	0.316	7.569	0.007
Elder 1	13.5	0.244	1, 146	0.244	4.931	0.028	13.5	0.003	1, 143	0.003	0.070	0.792
Elder 2	16.9	0.332	1, 146	0.332	6.695	0.011	16.9	0.001	1, 143	0.001	0.033	0.856
August 2001												
Skunk	0.55	0.087	1, 155	0.087	1.671	0.198	0.55	0.136	1, 157	0.136	1.833	0.178
McKinley	0.59	0.030	1, 155	0.030	0.573	0.450	0.59	0.048	1, 157	0.048	0.645	0.423
Barnwell	2.0	0.002	1, 155	0.002	0.039	0.844	2.0	0.077	1, 157	0.077	1.042	0.309
Fox	2.8	0.920	1, 155	0.920	17.764	<0.001	2.8	0.463	1, 157	0.463	6.248	0.014
Jack of Hearts	9.9	0.011	1, 155	0.011	0.204	0.652	9.9	0.883	1, 157	0.883	11.924	<0.001
Elder 1	13.5	0.117	1, 155	0.117	2.251	0.136	13.5	0.021	1, 157	0.021	0.278	0.599
Elder 2	16.9	0.099	1, 155	0.099	1.903	0.170	16.9	0.004	1, 157	0.004	0.057	0.813

Notes: "DA" is drainage area. The effect of grazing within individual sites was determined using orthogonal contrasts (Sokal and Rohlf 1995, SAS Institute 2001).

production (Finlay 2001, McNeely et al. 2006). As stream size increases, algae become more available as food to vulnerable primary consumers and generalists despite intense grazing by armored taxa (Finlay 2001, McNeely et al. 2006). Food chains lengthen and the dynamics of algal-based food webs may become more complex (e.g., Power 1990b).

The duration of strong grazing through the summer varied among streams with drainage areas greater than the 1-km² threshold. The persistence of armored grazer populations depended in part on the life history of the dominant grazer taxa. In sites in which the dominant armored grazers were univoltine, algae were released from grazing effects in late summer (Table 1, Fig. 5), following pupation of caddisflies and an order of magnitude decrease in grazer biomass (Fig. 3). Two of the dominant armored grazers, *Neophylax rickeri* and *Dicosmoecus gilvipes*, are univoltine, and their populations and grazing effects declined substantially as individuals completed their development and entered prepupal diapause. Armored grazer biomass dropped precipitously over the summer at sites in which univoltine species were dominant (Jack of Hearts and Elder Creeks, DA \geq 10 km²; Figs. 2 and 3). In late summer, there was no relationship between biomass of active larval grazers and relative primary productivity, and grazing limited epilithic biomass at only one site, Fox Creek (DA = 2.8 km²). At this site, *Glossosoma penitum* larvae remained dense through the summer. Although *Glossosoma* larvae were also abundant in Barnwell Creek in early summer, their densities declined, despite the continued appearance of early instar larvae. It remains unclear why *Glossosoma* populations differed from one another in their persistence. Rosemond et al. (2000) also found strong armored grazer (snail) control of algae throughout the growing season in a small,

forested stream. Differences in the relative persistence of armored grazers among sites may have consequences for the flow of algal carbon and energy through food webs, as they can compete with more vulnerable primary consumers (Kohler and Wiley 1997, Kuhara et al. 2000, McNeely et al. 2007) and reduce predator growth as a result (Power 1995).

Landscape thresholds in grazing regimes are likely explained by changes in multiple habitat factors that vary with drainage area. Canopy cover generally declined with drainage area, and water temperature, stream width, and primary productivity generally increased (Table 1, Fig. 4). Higher productivity allowed larger total populations of armored grazers, at least in early summer. Warmer stream temperatures and higher algal productivity both may have contributed to species turnover within the armored grazer guild. Larger, faster growing univoltine species may require warmer water temperatures and greater food availability to complete their development than are found in the smaller (DA < 5 km²) streams. Drainage area, because it integrates multiple habitat variables, may work well as a predictor of species interactions over landscape scales.

Although variation in tile biofilm biomass (AFDM) provides good evidence for the patterns in grazing effects described above, variation in chlorophyll *a* was less consistent. There are at least two plausible explanations for this difference. First, biofilms in some of the smaller, less productive streams may be made up largely of terrestrial detritus and heterotrophic microbes, with relatively little algae (Lock et al. 1984, McNeely et al. 2006). Studies of caddisfly diet suggest that the armored grazers abundant in our study sites assimilate primarily algae (Mayer and Likens 1987, Finlay 2001, McNeely et al. 2006). As they feed, however, the animals may detach non-algal biofilm material (Steinman 1996, Kuhara et al.

2000). In the two smallest, least productive streams in which we did observe grazer effects, we also observed reductions in chlorophyll *a* per area on at least one sampling date (July for Barnwell Creek, August for Fox Creek), suggesting that caddisflies affected abundance of algae as well as allochthonous and heterotrophic components of biofilms. In the larger streams within our survey, biofilms are dominated by algae (McNeely et al. 2006). Another explanation for inconsistencies between responses in biomass and chlorophyll is that grazing reduced senescence and siltation of algal biofilms, resulting in higher chlorophyll *a*/biomass on grazed tiles. Grazed biofilms often have higher chlorophyll/biomass and a greater proportion of live algal cells than ungrazed ones (Connor and Teal 1982, Power 1990a, 1992b, Steinman 1996). Light grazing by low densities of grazers and high densities of shredders is one explanation for the puzzling result of more chlorophyll *a* on grazed than exclusion tiles from Jack of Hearts Creek in August. This stream had especially high densities of large shredder caddisflies (*Psychoglypha*, *Hydatophylax*, and *Heteroplectron*) during late summer (McNeely 2004), and we observed them on control tiles. Although shredders lack biofilm-scraping mouthparts (Cummins and Klug 1979, Wiggins 1996), they likely removed sediment from unprotected tiles as they moved around and may have consumed some algae. Activity of non-grazing caddisflies can increase abundance of algae in drift, suggesting they bioturbate algal biofilms (Barnese and Lowe 1992). Removal of sediment and light grazing by these detritivores may have benefited algae by reducing light and nutrient limitation (similar to the effects observed by Power [1990a]).

Grazing regimes varied with drainage area as anticipated in our hypotheses, but the mechanisms differed from those predicted. We hypothesized that in larger streams earlier pupation of univoltine caddisfly larvae might allow earlier recovery of algae. In contrast, the pattern appears to result from species turnover within the armored grazer guild. Multivoltine *Glossosoma* were replaced by univoltine *Dicosmoecus* and *Neophylax*. In regions with different species pools, the effects of species turnover may be different. However, the transition from algal food webs with one to two trophic levels is likely to be widespread in forested watersheds, although the threshold for this change will likely vary among regions with different vegetation, climate, topography, or land use. Mapping changes in ecological interactions onto drainage area gradients in stream networks is likely to be an effective way of probing the impacts of environmental conditions on species interactions.

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APPENDIX

Regression equations used to estimate biomass of caddisflies from case length (*Ecological Archives* E088-157-A1).