Shifts in habitat templates for lotic microalgae linked to interannual variation in snowmelt intensity

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Abstract

We investigated the importance of snowmelt as an organizing factor for epilithic microalgae in a high-altitude montane stream during 3 yr (1995–1997) of differing melt characteristics. Changes in algal biomass and taxonomic structure in two stream reaches that differed in hydrologic characteristics were assessed relative to variation in stream-water nutrient content, temperature, surface-water/groundwater exchange, and algivorous macroinvertebrate assemblages. Melt-induced increases in stream discharge were large and abrupt in 1995, nearly undetectable in 1996, and protracted and of intermediate magnitude in 1997. In 1995, algal and grazer densities were significantly reduced by melt discharge. Postmelt grazer recovery was slow, and the percentage of live cells in the diatom assemblage increased abruptly; algal biomass initially increased and subsequently varied with stream-water N : P ratio. In 1996, snowmelt produced no evident proximate effects. Initial high grazer densities declined throughout the summer. In midsummer, an N : P ratio of 140 in the upstream reach corresponded to a more than fourfold increase in algal biovolume and a shift to dominance by large diatoms. Downstream, a lower N : P peak induced no algal response. In 1997, grazer densities declined during protracted melt runoff and increased sharply during melt recession, concurrent with decreases in live diatom percentage and algal biovolume. N : P declined in 1997 from ~16 : 1 to values indicative of N limitation and correlated with decreases in algal biovolume. Our results show that effects of snowmelt in montane streams reflect both initial melt-induced mortality that sets initial conditions for succession and melt-induced aquifer recharge that controls nutrient supply in the months following peak melt discharge. The influence of these two components extends beyond snowmelt recession into summer base flow, suggesting that variation in melt characteristics generates interannual differences in the functioning of these systems.

Patterns of temporal and spatial variation in communities of primary producers are underlain by a template of physical, chemical, and biological factors. These factors act individually or interactively to dictate taxonomic structure, biomass, and community dynamics. This "habitat template" shifts within years in response to seasonal changes in the physical/chemical environment (Duncan and Blinn 1989) and the phenology or timing of visitation by herbivores (Jacoby 1987). Shifts can also be induced by stochastic episodes of physical disturbance (Zimmerman et al. 1996) that modify the template on multiple levels or by pathogen outbreaks that alter the biological component (Peterson et al. 1993). Variation in global weather, such as the El Niño-Southern Oscillation phenomenon, induces differences among years in seasonal precipitation and temperature and in the frequency and magnitude of flood disturbance (Molles and Dahm 1990). Thus, change in a habitat template within a given year, and consequent changes in the dynamics of ecological communities, can be strongly influenced by broader-scale climatic properties.

In stream ecosystems, within- and among-year variation in channel discharge influences many factors that characterize the habitat template for benthic algae, the major source of autochthonously fixed carbon in these systems. Young and Huryn (1996) noted that a 310-km continuum of the Taieri River, New Zealand was autotrophic along its length in a year of relatively low average discharge but was autotrophic in only the upper 70 km during a high-discharge year, owing to differences in turbidity and light availability. Abrupt increases in stream discharge can reduce standing crops of benthic algae and their consumers (Grimm and Fisher 1989) but lower resilience of consumer populations can allow subsequent accrual of algal biomass (Power 1992). Flood events are also often associated with transient (days to weeks) increases in water-column nutrient concentrations, but floodwater nutrient loads can vary depending on flood timing. For example, floods that occur after prolonged drought in the Sonoran Desert carry higher dissolved N loads than those occurring after frequent rainstorms have depleted the soil of stored nitrogen (Grimm and Fisher 1991). Stream discharge also affects spatial and temporal variation in the strength and direction of hydrologic exchange between surface water and groundwater, directly influencing the degree to which subsurface biogeochemical processes affect the pool of dissolved nutrients available for microbial uptake (Dahm et al. 1998).

Table 1. Minimum and maximum values of physical and chemical variables for study periods over 3 yr in Rio Calaveras.

	18 April–25 July 1995		23 April–6 August 1996		22 April–1 July 1997	
	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
Temperature (°C)	8.1–14.3	7.6–12.5	10.8–15.7	10.0–14.2	10.7–14.1	9.5–12.5
TIN (μg L^{-1})	17–150	34–100	23–184	8–73	39–136	14–93
SRP (μg L^{-1})	<3–32	<3–17	<3–11	4–13	13–19	14–25
N:P	5.6–22.9	3.3–28.2	5.8–140.2	1.8–38.9	5.9–19.1	2.0–13.9

The depth and spatial variation of snowpack and the timing and intensity of snowmelt-induced runoff in montane streams can vary significantly among years. Lewis and Grant (1980) noted that postmelt concentrations of dissolved NO_3-N in surface waters of streams within an alpine catchment varied inversely with mean depth of snowpack, a result that Brooks et al. (1998) demonstrated could arise from higher N retention by soil microbes under deep, persistent snow cover relative to years when snow cover was more heterogeneous. The timing and rate of snowmelt can also influence solute concentration in meltwater. Williams et al. (1996*b*) reported that NO_3-N concentrations in meltwater, relative to that in snow, were four times higher in a year with a delayed, discontinuous snowmelt than with an earlier, more rapid melt during the previous year.

Although snowmelt is predictable within an evolutionary context of species life-history attributes, the proximate effects of melt-induced increases in stream discharge on stream biota and hydrology should depend on melt intensity, which can vary substantially among years (Poff and Ward 1989). Higher magnitude events should be associated with more extensive scour of the benthos and greater recharge of groundwater aquifers. Subsequent spatial and temporal variation in benthic community dynamics and in the strength and direction of hydrologic exchange between groundwater and stream surface waters (and consequent variation in supply of dissolved nutrients—cf. Valett et al. 1994) should vary with the timing, magnitude, and duration of spring snowmelt. Here we present data collected from two reaches, 75 m apart, in a small montane stream in the southwestern United States during 3 consecutive yr that differed dramatically in snowmelt characteristics. Data published by Wroblicky et al. (1998) indicated that, since discharge in this stream varies, groundwater–surface water interactions within our two study reaches differ substantially. We hypothesized that such differences would generate spatial heterogeneity in nutrient supply, the nature of which should depend on the degree to which the groundwater aquifer is recharged by snowmelt. Furthermore, we expected characteristics of biotic assemblages immediately after peak melt discharge to vary with snowmelt intensity, influencing the response of biota to temporal changes in hydrology and nutrient supply. In this context, we investigate the importance of spring snowmelt as an organizing factor for epilithic microalgae in high-altitude montane systems.

Methods

Study site—This study was conducted in Rio Calaveras, a first-order tributary to the Jemez River originating at an al-

titude of 2,475 m in the Jemez Mountains of north central New Mexico, United States. Our two study reaches, one located 6–25 m below the spring source (henceforth the "upstream reach") and a second 102–150 m from the spring source ("downstream reach"), meander through open meadow bordered by mixed coniferous forest (predominantly blue spruce, *Picea pungens,* and Ponderosa pine, *Pinus ponderosa*), and are of similar depth (10–15 cm) and base-flow current velocities (5–10 cm s^{-1}). Base-flow discharge in these reaches ranged from 0.6 to 3.0 L s^{-1}. Streambed material consists of small (long axis 3–10 cm) cobbles derived from alluvium of volcanic tuff, intermixed among smaller gravels and silts.

Sample collection and processing—Samples of epilithic algae, cobble-associated macroinvertebrates, and stream water for determining concentrations of dissolved inorganic nitrogen (ammonium-N [NH_4-N] and nitrate-N [NO_3-N], combined and reported as total inorganic nitrogen [TIN]) and soluble reactive phosphorus (SRP) were collected from each reach at 1–4 week intervals from mid-April to late July/early August in 1995 and 1996 and to 1 July in 1997 (Table 1). Algae and macroinvertebrates were collected throughout each reach, as described below; stream-water samples were taken at the head of each reach. NO_3-N concentrations were determined by use of an ion chromatograph (Dionex Dx-100) equipped with a conductivity detector for anion analysis. SRP and NH_4-N were analyzed with a Technicon AutoAnalyzer, following protocols of Murphy and Riley (1962) and Soloranzo (1969), respectively. Water temperature was measured at each reach head by use of a digital temperature probe. Direction and magnitude of the vertical hydraulic gradient (VHG) was measured in 1.27-cm diameter PVC minipiezometers, placed at ~2-m intervals down the length of each reach. Positive VHG values denote groundwater discharge into the surface stream (i.e., upwelling) and negative values reflect recharge sites (downwelling).

Four (in 1995) or three "composite" samples of algae and macroinvertebrates were collected in each reach on each sampling date. Each composite combined biota from three randomly selected cobbles. Macroinvertebrates retrieved with a 200-μm mesh dip net placed downstream of a collected cobble and those picked from cobble surfaces were preserved in 95% ethanol for later identification and enumeration. Cobbles were transported on ice to the laboratory, where epilithon from each three-cobble composite was removed with a toothbrush and wash bottle, creating a slurry that was subsampled for quantitative measures of ash-free dry mass ([AFDM] dried at 60°C for 4 h; ashed at 500°C

for 4 h) and chlorophyll *a* (after Wetzel and Likens 1979) and for preparation of syrup mounts (after Stevenson 1984) to determine algal cell densities, biovolume, and taxonomic structure. Surface areas of collected cobbles, used to calculate algal and macroinvertebrate densities, were estimated by regression of aluminum foil weight and area on foil wrapped over exposed cobble surfaces.

Algal cell densities, taxonomic structure, and biovolumes were determined by counts and identification, at 1,250× magnification, of at least 500 chloroplast-containing algal cells from each sample. Concurrently, dead diatom cell densities were determined by enumerating all single diatom valves bearing a central area and the two valves of intact but empty diatom frustules and dividing the total number of valves counted by two. Together, live and dead diatom counts were used to calculate the percentage of diatom cells within each sample that were presumed living at the time of collection (% live diatoms). Biovolumes were estimated for each algal taxon from measurements of ≥10 cells for common taxa, or two cells for rare taxa, by use of geometric formulae approximating cell shapes (Hillebrand et al. 1999).

Data analysis—Between-reach differences in algal (AFDM, chlorophyll, cell density, biovolume, and % live diatoms) or macroinvertebrate (densities of grazing caddisfly larvae, mayflies, or chironomids) variables were detected with a two-factor (site) repeated-measures (with date) analysis of variance for each year. All density data were natural-log transformed prior to analysis to normalize variance; % live diatom data were arcsine–square-root transformed.

We used stepwise multiple linear regression, using the MAXR option (Statistical Analysis System 1990), to examine the strength of relationships between algal variables and potential physical (temperature), chemical (TIN, SRP, and N : P ratio), or biological (caddisfly, mayfly, and chironomid densities) control factors for each year.

Detrended correspondence analysis (DCA) was employed to examine variation in algal taxonomic structure in epilithic assemblages between reaches and among years. Samples were ordinated by use of relative biovolumes of common (those averaging ≥5% of total algal biovolume of at least one site on one date) algal taxa. In this analysis, the greater the distance between samples in a two-dimensional ordination plot, the larger the difference in algal taxonomic structure between those samples. Species ''loadings'' along each of the two primary axes illustrate which taxa were most influential in positioning samples in a given area of the ordination.

Results

Variation in hydrologic, physical, and chemical attributes—Snowmelt runoff and the frequency and intensity of rainfall, differed considerably among the 3 yr of this study, generating postmelt variation among years in stream-water nutrient content and in the strength and direction of surface/subsurface hydrologic exchange (Table 1, Fig. 1). In 1995, premelt precipitation raised discharge in Rio Calaveras from 2.9 L s^{-1} at the downstream reach on 4 April to 4.9 L s^{-1} 2 wk later. Melt of a relatively heavy snowpack on 2 May

increased stream discharge to 102 L s^{-1}. In 1996, snowmelt discharge was extremely low, elevating stream flow <0.5 L s^{-1} above a premelt base flow of 1.4 L s^{-1} (Fig. 1). The snowmelt-induced discharge increase in 1997 was appreciable but more protracted than that in 1995, resulting in discharge increases from 3.5 L s^{-1} on 1 April to 4.3, 6.6, 12.1, and 20.9 L s^{-1} in subsequent weeks, before finally peaking at 29.7 L s^{-1} on 13 May (Fig. 1). The 1995 summer precipitation records were incomplete, but the Rio Calaveras catchment did receive rainfall in mid-June (Valett pers. observation). Very little rainfall occurred between snowmelt and late July in 1996, with the only measurable precipitation falling on 9 July (0.8 mm) and on 4 of the last 5 d of July (1–4 mm). In contrast, precipitation was common during the summer of 1997; rainfall of 0.5 to 18 mm was recorded on 8 of the last 12 d of April, 13 of 31 d in May, 10 of 30 d in June, and 14 of 31 d in July.

Snowmelt intensity and frequency of precipitation were reflected in patterns of hydrologic exchange between surface and subsurface regions and spatial and temporal variation in relative nutrient availability (Fig. 1). Throughout the 1995 snowmelt, VHG measures reflected strong upwelling conditions along the length of the upstream reach. The downstream reach, on average, lost water to the subsurface (i.e., downwelling) for all but the single premelt and final postmelt sampling date. N : P ratios fluctuated similarly at upstream and downstream sites from values below 16 : 1 to values just above this ratio until N : P at the two reaches diverged in mid-June. In 1996, mean VHGs indicated that both reaches were downwelling throughout pre- and postmelt sampling, with VHGs consistently more negative upstream than down. Negative mean VHG data from the upstream reach, however, were heavily influenced by strong downwelling in the upstream-most peizometer, since VHG readings at other locations within this reach indicated upwelling. Although the direction of change in N : P ratios at the two reaches were similar, increases in N : P were much greater at the upstream reach, where high N (184 μg L^{-1}) and low P (<3 μg L^{-1}) generated an N : P spike of 140.2 on 9 July. In 1997, both reaches were generally upwelling on all but the final postmelt collection date, with VHG at upstream sites consistently higher than those downstream (Fig. 1). N : P ratios at both reaches exhibited premelt values of ~16 : 1 and declined steadily throughout the postmelt period.

Variation in densities of grazing macroinvertebrates—Densities of cobble-associated macroinvertebrates varied considerably between reaches and during pre- and postmelt periods among years (Fig. 2). Taxa considered to consume epilithon as a major component of their diet included non–filter-feeding, nonpredacious caddisfly larvae (mostly *Glossosoma* and *Agapetus* [Glossomatidae]), mayfly nymphs (mostly *Cinygmula* and *Leucrocuta* [both Heptageniidae], *Baetis* [Baetidae], and *Ameletus* [Ameletidae]), chironomid larvae, and the amphipod *Hyalella azteca*. These ''grazing'' taxa made up >40% of the macroinvertebrate assemblage on all collection dates and >70% of that assemblage on 31 of 42 collection dates. Samples with relatively low grazer densities typically contained high percentages of filter-feeding blackfly larvae (Diptera [Simuliidae]). In all years, chi-
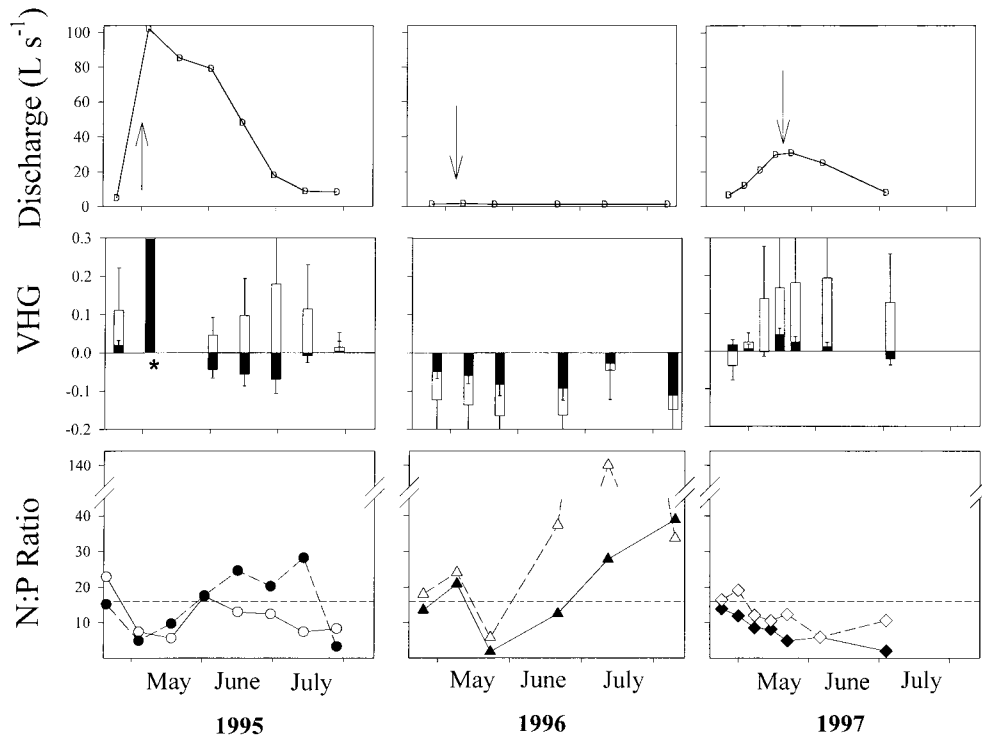
Fig. 1. Discharge in the downstream reach, N : P ratio, and mean VHG (±1 SE) within upstream (open symbols/bars) and downstream (closed symbols/bars) study reaches during study periods in 1995, 1996, and 1997. Horizontal line demarks an N : P ratio of 16 : 1, identifying the theoretical threshold between P and N limitation. Arrows identify timing of peak snowmelt in each year. * VHG >0.60.

ronomid larvae tended to be more abundant than caddisflies and mayflies on collection dates later in the summer (Fig. 2), although significant temporal changes in chironomid densities were noted only in 1995 (Table 2).

The 1995 snowmelt significantly reduced densities of all major grazer groups (Fig. 2). Mayfly and chironomid densities increased after peak melt discharge, with mayflies more abundant downstream than upstream (Fig. 2, Table 2). *Ameletus* and *Cinygmula* made up the bulk of premelt mayfly assemblages whereas, in late June and July, *Cinygmula* alone dominated. Densities of grazing caddis larvae remained low after melt-induced reductions in 1995.

In 1996, minimal discharge increase associated with snowmelt had no obvious effects on grazer densities (Fig. 2). Both caddisfly and mayfly densities declined steadily throughout the postmelt collection period (Fig. 2, Table 2). Grazing caddis contributed 35.5% (±7.9% SE) to premelt grazer assemblages in the downstream reach and 24.1% (±4.1%) upstream but were absent downstream and had dropped to 4.2% (±1.1%) upstream by 6 August. Concurrently, contribution of mayflies to the grazer assemblage fell from 41.6% (±7.6%) to 10.6% (±4.9%) in the downstream reach and from 35.4% (±7.9%) to 10.1% (±3.3%) upstream. As in 1995, *Cinygmula* and *Ameletus* were the predominant mayfly taxa in April and May. Chironomid densities fluctuated with time and exhibited high variation among replicates on most dates (Fig. 2). Accordingly, no significant change in chironomid density was associated with the 1996

melt (Table 2). The relative contribution of chironomids to the grazer assemblage, however, increased substantially from a premelt contribution of 15.9% (±9.0%) to 84.3% (±7.7%) by 6 August in the downstream reach and from 35.0% (±9.7%) to 85.7% (±4.0%) upstream.

In 1997, caddisfly, mayfly, and chironomid densities declined in the 3–4 wk prior to peak snowmelt in 1997 (Fig. 2), a period of gradual increase in discharge (Fig. 1). In contrast to patterns observed in 1996, abundances of caddis and mayflies increased over time after peak discharge. For grazing caddis, differences in the pattern of change between reaches yielded a significant site/date interaction in 1997 (Table 2). High mayfly densities in June and July were comprised primarily by *Baetis* and *Leucrocuta*. Chironomid densities varied substantially within and among dates (Fig. 2); contributions by chironomids to the grazer assemblage were greatest in May and June (65.1%–97.7%) and lowest on 1 July (38.3% ± 13.9% downstream; 49.6% ± 5.9% upstream).

Variation in biomass and taxonomic structure of epilithon—Patterns of temporal change in epilithic biomass and taxonomic content differed considerably in pre- and postmelt periods among years. AFDM and Chl *a,* broad measures of epilithon biomass and its algal component, varied similarly in all 3 yr (Fig. 3, Table 2). Epilithic biomass was reduced significantly by snowmelt in 1995 but increased throughout all or most of the postmelt recovery period; recovery pat-
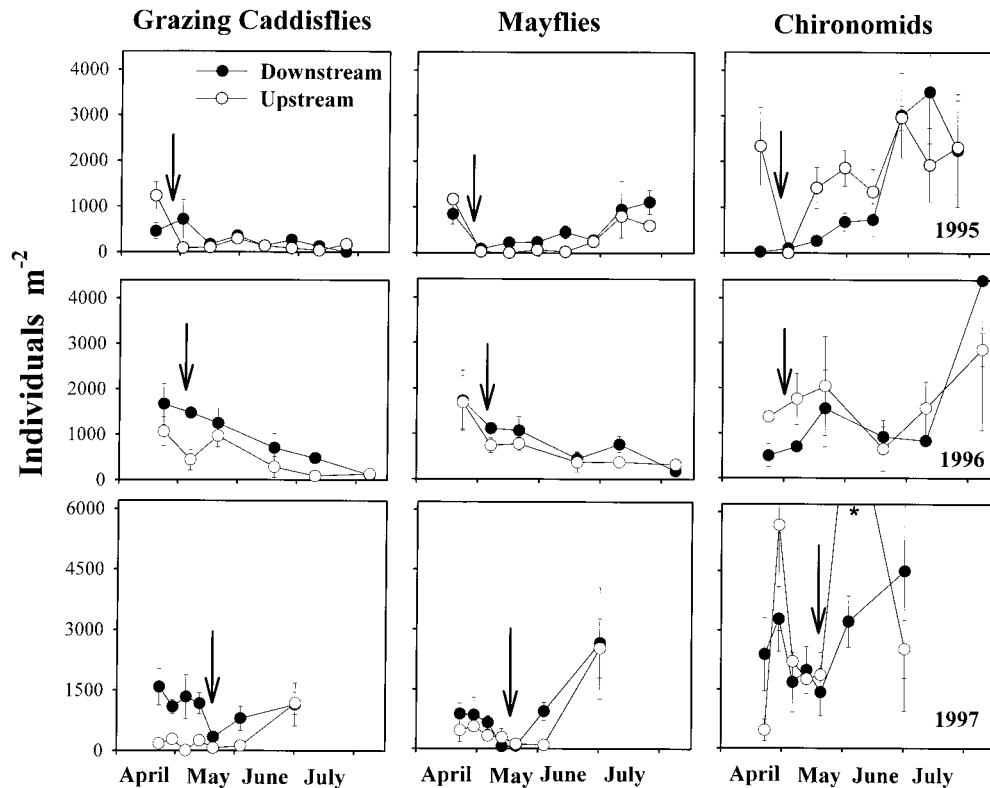
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Fig. 2.   Densities (±1 SE) of the three dominant groups of cobble-associated grazing macroin-
vertebrates in upstream and downstream study reaches during study periods in 1995, 1996, and
1997. Arrows denote time of peak snowmelt discharge. Off-scale 1997 chironomid density (denoted
"*") = 9,110 ± 1,395 SE.

terns did not differ significantly between reaches. In 1996, snowmelt had no discernable effect on any measure of algal biomass, but AFDM increased significantly postmelt, and both AFDM and chlorophyll were significantly higher in the upstream reach than downstream. In 1997, both AFDM and chlorophyll dropped precipitously throughout the collection period in both reaches (Fig. 3, Table 2).

Algal biovolume and cell densities in the study reaches changed similarly within each year, but patterns of change varied among years, as did the dominant algal taxa (Table 3). In 1995, both biovolume (Fig. 4) and cell densities (Fig. 3) were reduced significantly by snowmelt, generally increased during postmelt recovery and were higher upstream than downstream (Table 2). Algal biovolume and N:P ratio were significantly correlated in both upstream and downstream reaches, except during 1996 (Fig. 4). In 1995, diatoms made up the largest percentage of algal biovolume on all dates in both reaches, except downstream on 11 July,

Table 2.   Results of two-factor (Site) repeated-measures (with date) ANOVA* on algal and macroinvertebrate data from mid-April to July/early-August collections from Rio Calaveras in 3 yr (see text for specific range of dates). Probabilities that are in boldface type are significant at $P < 0.05$. All variables were natural-log transformed before analysis, except for % live diatoms, which was arcsine–square-root transformed.

Variable	1995			1996			1997		
	Site	Date	SD	Site	Date	SD	Site	Date	SD
Ash-free dry mass	0.224	**0.002**	0.340	**0.004**	**0.001**	0.148	0.839	**<0.001**	0.874
Chl *a*	0.200	**0.002**	0.134	**0.043**	0.264	0.219	0.337	**<0.001**	0.231
Algal biovolume	**0.028**	**<0.001**	0.190	**<0.001**	**0.014**	0.143	0.165	**<0.001**	0.249
Algal cell densities	**0.014**	**<0.001**	0.217	**0.003**	0.680	0.978	0.197	**<0.001**	0.302
% live diatoms	0.405	**<0.001**	**0.024**	**0.004**	0.076	0.960	0.054	**<0.001**	0.455
Caddisfly	0.715	**<0.001**	**0.037**	0.058	**0.009**	0.074	**0.011**	**0.001**	**0.006**
Mayfly	**0.002**	**<0.001**	**0.001**	0.324	**0.034**	0.708	0.428	**0.037**	0.456
Chironomid	0.137	**<0.001**	**<0.001**	0.441	0.105	0.255	**0.012**	0.169	0.952

* Between-group degrees of freedom for 1995 =1,6 and for 1996 and 1997 =1,4. Degrees of freedom for within-group effects for 1995 =7,42; for 1996 =5,20; and for 1997 =6,24.
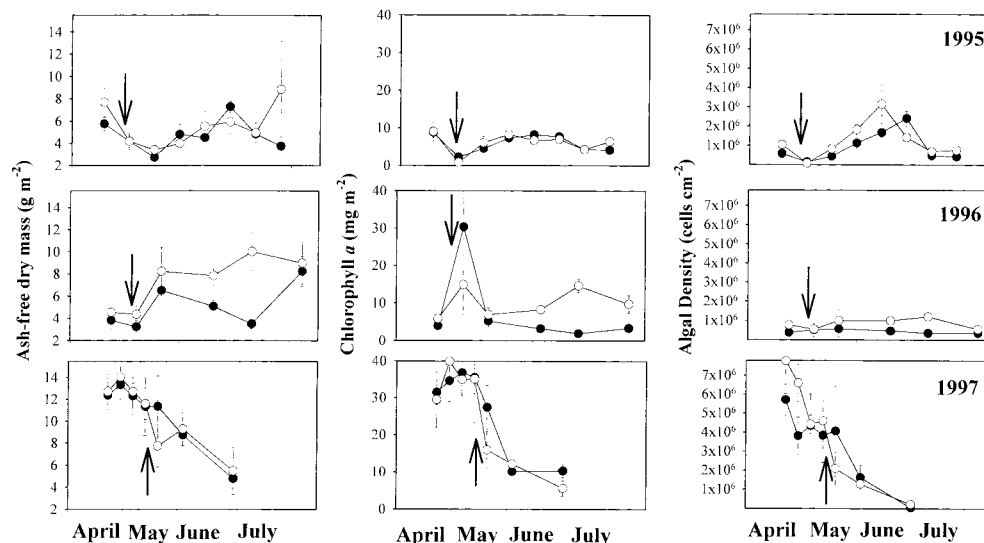
Fig. 3. Mean epilithic biomass ($\pm$1 SE) as AFDM, Chl *a,* and algal cell density in upstream and downstream study reaches during study periods in 1995, 1996, and 1997. Arrows denote time of peak snowmelt discharge.

when a consortium of filamentous green algae and associated basal cells dominated (Fig. 4). Changes in algal taxonomic structure followed similar trajectories in both reaches across the 1995 snowmelt and into postmelt recovery (Fig. 5). The adnate diatom, *Planothidium lanceolatum,* increased in relative biovolume at the upstream reach from 9.0% in premelt samples, to 26.2% at peak discharge, to 37.3% in the first postpeak sampling. *Navicula arvensis,* a very small diatom,

increased from contributing 0.4% to algal biovolume upstream on 18 April, to 1.1% at peak discharge, to 14.1% on 16 May. If measured as relative abundance rather than biovolume, *N. arvensis* accounted for an average of 33.7% of all cells encountered from 16 May samples, with a maximum in one of four upstream replicates of 61.9%. Patterns of change in taxonomic structure during postmelt recovery were similar in both reaches, with 25 July samples lying in

Table 3. Minimum and maximum relative biovolumes (% of total) of common algal taxa encountered in composite epilithon samples taken during sampling periods in 1995, 1996, and 1997. Species codes apply to the ordination presented in Fig. 5.

| Species	Code	Relative biovolume (min–max)		
		1995	1996	1997
Achnanthidium minutissimum	ACMI	5.5–25.3	0.9–17.2	6.1–40.4
Cocconeis placentula	COPL	0–1.1	0.2–7.7	2.6–11.1
Fragilaria leptostauron	FRLE	0–6.5	0.9–5.2	2.2–11.0
Fragilaria pinnata	FRPI	0–7.4	0–6.1	0–3.2
Fragilaria pinnata var. *lancetula*	FRPL	0–9.1	1.9–16.7	2.0–28.7
Gomphonema angustatum	GOAN	0.3–21.8	0.1–3.6	0.2–10.3
Gomphonema parvulum	GOPA	0.2–8.8	0–4.5	0–1.8
Gomphonema cf. *rhombicum*	GORH	0–0.9	0–11.3	0–12.8
Gomphonema truncatum	GOTR	0–1.1	0–37.8	0–7.4
Navicula arvensis	NAAR	0.3–14.1	0.01–0.8	0–0.5
Navicula lanceolata	NALA	0–1.2	0–6.2	0–1.6
Navicula tantula	NATA	0.4–6.0	0.5–7.3	0.9–5.6
Nitzschia linearis	NILI	0–9.6	0–4.0	0–5.2
Planothidium lanceolatum	PLLA	5.3–37.3	0.8–12.5	2.5–9.4
Reimeria sinuata	RESI	0.2–5.6	0–1.4	0.1–1.8
Rhoicosphenia curvata	RHCU	0.2–6.5	0.3–4.0	0.9–4.0
Synedra rumpens var. *meneghiniana*	SYRU	0.6–11.8	0–0.8	0–4.6
Synedra ulna	SYUL	0–6.4	0–38.8	0–0.4
Chroococcus sp.	CHRO	0.1–3.9	0.5–10.0	2.3–19.9
Schizothrix sp.	SCHI	0.1–7.0	0.04–2.6	0.5–6.1
Green algal basal cells	GRBA	4.3–31.8	2.0–30.4	2.7–8.6
Green algal filaments*	GRFL	0–14.3	0–0.9	0–3.9

* Primarily *Stigeoclonium.*
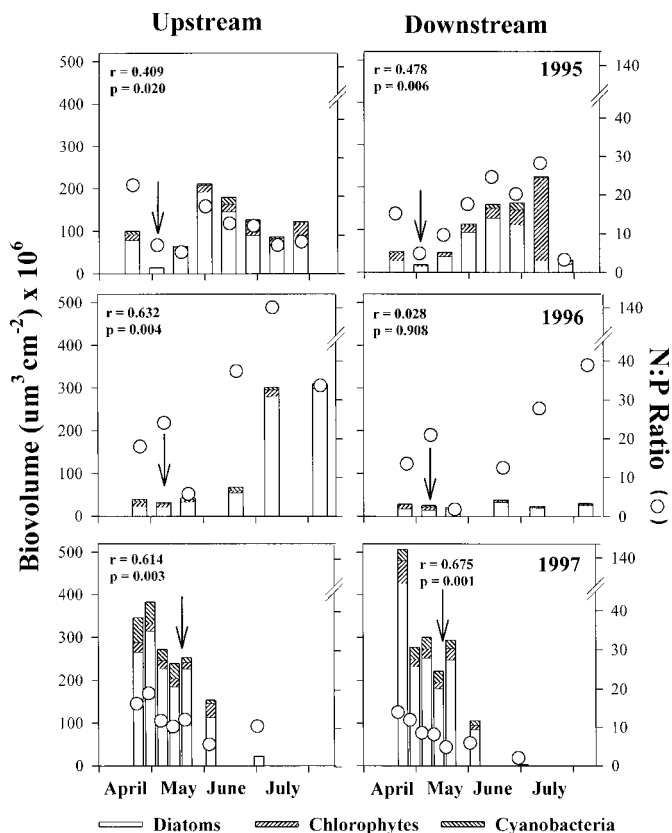
Fig. 4. Epilithic algal biovolume, partitioned among divisions (diatoms, chlorophytes, and cyanobacteria), and stream-water N:P ratios in upstream and downstream study reaches during study periods in 1995, 1996, and 1997. Pearson correlation coefficients (*r*) between total biovolume and N:P ratio, and their significance levels (*P*) are presented in each panel. Arrows denote time of peak snowmelt discharge.

ordination space heavily influenced by filamentous green algae (primarily *Stigeoclonium*) (Fig. 5).

Snowmelt in 1996 had no discernable proximate effect on epilithic algal biovolume (Fig. 4) or cell densities (Fig. 3). Biovolume in the upstream reach increased over time (Table 2, Fig. 4), concurrently with a large increase in N:P ratio. This biovolume increase was produced, primarily, by proliferation of large-celled diatoms, *Synedra ulna, Gomphonema truncatum,* and, less dramatically, *Nitzschia linearis* at the time of the increase in N:P ratio (Table 3, Fig. 5). TIN was greater at upstream sites on five of six dates, and average concentration upstream was >1.8 times that observed downstream during premelt and the 3 months of postmelt collections. Biovolume in the downstream reach remained uniformly low (Fig. 4), but changes in taxonomic structure indicated by ordination suggested a trajectory similar to that observed upstream (Fig. 5) in tandem with much smaller increases in N:P ratio (Fig. 1).

In 1997, premelt algal biovolume (Fig. 4) and cell densities (Fig. 3) were higher than those in premelt samples from 1995 or 1996. Both measures were statistically similar between reaches but declined over time (Table 2) as N:P ratios decreased (Fig. 4). Small, chain-forming species of the

diatom genus *Fragilaria* (=*Staurosirella*), adnate diatoms *Achnanthidium minutissimum* and *Cocconeis placentula,* and the small, coccoid cyanobacterium *Chroococcus* were more abundant in 1997 samples than other years (Table 3), clustering 1997 samples in the lower central portion of DCA ordinations (Fig. 5).

Percentages of live cells in diatom assemblages were relatively high in 1995, particularly in the weeks after snowmelt (Fig. 6), then decreased to ~50% by late July. In 1996, live cell percentages were low throughout the sampling period and exceeded 50% only in samples taken upstream in June and July. In 1997, 58%–71% of diatom cells within samples were live until 1 July, when live cell percentages dropped below 45% (Fig. 6), concurrent with density increases of mayflies and grazing caddis (Fig. 2).

Relationship between algal variation and algal control factors—The suite of physical, chemical, and biological factors influencing epilithic algal communities during pre- and postmelt sampling varied among years and among algal-response variables (Table 4). For 1995 AFDM and Chl *a* data collected in the downstream reach, 59.3% and 42.5% of the variation, respectively, was explained by multiple linear regression models that incorporated primarily chemical variables and temperature. Upstream, variation in densities of caddisfly larvae and, less strongly, mayflies influenced these response variables. Variation in more specific metrics (algal biovolume, cell densities, and diatom live-cell percentages) was explained well by a combination of chemical, physical, and biological variables in the upstream reach (Table 4). Downstream, however, regression models explained less variation, and chemical factors loaded heavily with cell densities and algal biovolume. Shifts in algal taxonomic structure, quantified with changes in sample distribution on DCA axes, could not be attributed to variation in any set of independent variables in the downstream reach (Table 4). Upstream ordination scores varied with changes in N:P ratio, TIN, and mayfly densities. For 1996 data, significant regression models, incorporating a combination of biotic and abiotic variables, were generated for all algal-response variables in the upstream reach. Downstream, of the four algal biomass metrics, only AFDM yielded a significant model (Table 4). Variation in ordination scores was explained well by one- to three-variable models incorporating combinations of temperature, caddisfly density, N:P ratio, TIN, and SRP. In 1997, the more general biomass metrics varied with TIN in the downstream reach, whereas upstream variation in chlorophyll exhibited a weak inverse relationship with temperature. Variation in algal density metrics was best explained in the upstream reach by changes in grazer densities and streamwater N:P ratio and downstream by TIN, temperature, and/or caddisfly density (Table 4). Diatom live-cell percentages in the downstream reach varied with streamwater chemistry and temperature. Shifts in algal taxonomic structure during 1997 were not well explained by any combination of abiotic or biotic control factors.

Discussion

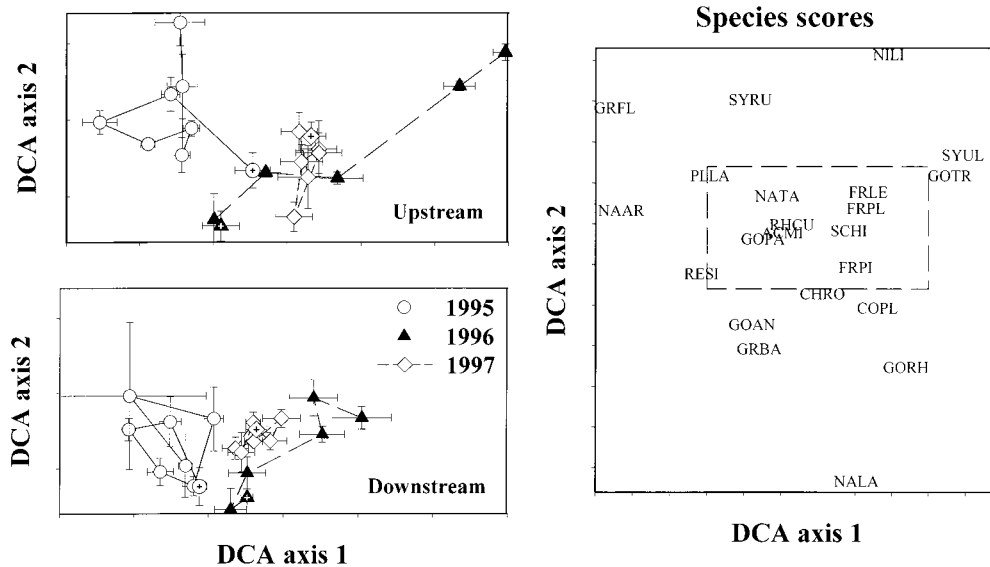*Snowmelt as a disturbance: proximate effects*—Our results show that initial effects of snowmelt runoff and sub-

Fig. 5. Mean sample scores (±1 SE) along DCA ordination axes defined by relative biovolume of common algal taxa in epilithic samples collected from upstream and downstream study reaches during study periods in 1995, 1996, and 1997. Initial premelt samples are denoted with a plus sign (+). Species loadings for taxa used in the analyses are given in the right panel, with the dashed rectangle within delimiting the extent of axis scores from the sample plots. See Table 3 for identification of species abbreviations.

sequent interactions between biological, physical, and chemical factors that affect stream communities during summer base flow are strongly influenced by year-to-year variation in snowmelt intensity. Although the occurrence of spring snowmelt is a predictable yearly event that clearly has influenced the evolution of life history attributes of biota in montane streams (Poff 1992), the response of populations to this disturbance can vary markedly among years, depending on variation in the timing and magnitude of this event. Thus, stream community responses to snowmelt vary among years of differing melt characteristics, much as variation in severity of winter storms influences the structure and dynamics of kelp-forest communities (Dayton et al. 1992). Generation times of aquatic macroinvertebrates vary from weeks to months or, less commonly, to years (Wallace and Anderson 1996), and those of benthic microalgae can be measured in days (Stevenson and Pan 1996). Thus, proximate effects of

elevated melt-induced discharge, on microalgae in particular, should be analogous to that of any other flow-related disturbance.

Significant melt-induced reduction in algal biomass and changes in taxonomic structure were noted only in 1995. Of the 3 yr that we assessed biotic resistance to snowmelt in Rio Calaveras, this was the year when discharge increase was most abrupt and of the greatest magnitude. Algal assemblages sampled immediately after peak melt discharge in 1995 supported low cell densities and were dominated by small, adnate diatoms. Similar shifts to dominance by low-profile, tightly adherent taxa often follow scour disturbance induced by elevated flows (Blenkinsopp and Lock 1994) or exposure to intense grazing (Rosemond et al. 1993). Adnate diatom species typically reside at the base of epilithon, where access to light and inorganic nutrients can be low, and remain viable longer under such conditions than motile, stalk-forming, or colonial species (Moss 1977; Johnson et al. 1997). The transient postmelt increases in abundance of adnate taxa suggest stimulation of reproductive activity in basal taxa with increased access to light and water-column nutrients after removal of overlying algal biomass. This interpretation is supported by the dramatic postmelt increase in diatom live-cell percentage in 1995. This taxon-specific response is interesting, because premelt algal assemblages were already of relatively low biomass and had been exposed to grazer densities that other studies conducted in this system have shown to constrain algal densities (Peterson et al. 1998, in press). Resistance to intense grazing apparently does not always confer resistance to flow-related scour, since even extremely thin (e.g., <10 μm) biofilms exhibit observable physical damage from storm flows (Blenkinsopp and Lock 1994).
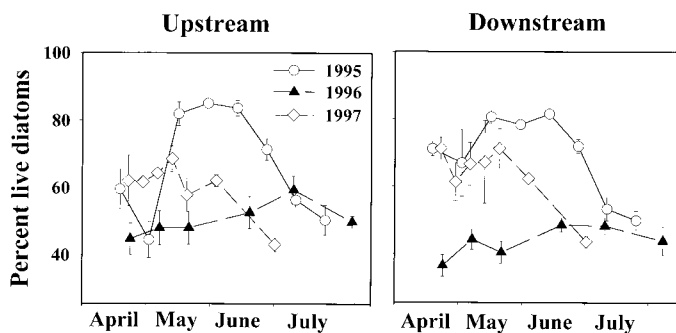

Fig. 6. Variation in mean diatom live-cell percentages (±1 SE) in upstream and downstream study reaches during study periods in 1995, 1996, and 1997.

Table 4. Stepwise multiple regression results for effects of physical, chemical, and biological variables on algal attributes in upstream and downstream reaches. The regression equation for each algal attribute was $Y = B_0 + B_{VAR1}X_1 + B_{VAR2}X_2... + B_{VARn}X_n$, where B_0 is **the intercept,** B_{VAR} are coefficients for each independent variable (X_n) retained in the model, and n is the number of variables included in the model to maximize R^2. % live diatoms was arcsine–square-root transformed prior to analysis; all other algal attributes and grazer densities were natural-log transformed. Sign and significance-level of coefficients are as follows: + or −, $0.05 > P > 0.01$; ++ or −−, $0.01 > P > 0.001$; +++ or −−−, $P < 0.001$. NS, not significant ($P > 0.05$).

Dependent variable	Indep. var. 1995	Upstr. Prob. 1995	Upstr. Model R² 1995	Downstr. Prob. 1995	Downstr. Model R² 1995	Indep. var. 1996	Upstr. Prob. 1996	Upstr. Model R² 1996	Downstr. Prob. 1996	Downstr. Model R² 1996	Indep. var. 1997	Upstr. Prob. 1997	Upstr. Model R² 1997	Downstr. Prob. 1997	Downstr. Model R² 1997
Ash-free dry mass	N:P		18.7	+++	59.3	TIN	++	38.2	−	56.3	TIN	NS	NS	+++	46.7
	TIN			+		Caddisfly	−−−		−						
	SRP			++		Mayfly									
	Temp			−−−											
	Mayfly	+		+											
	Midge														
Chl *a*	Temp	+++	69.9		42.5	N:P	+	23.9	NS	NS	TIN		28.7	+++	52.4
	Caddisfly	++									Temp	−−−		−	
	N:P	+		++											
	TIN			++											
Algal biovolume	TIN	−−	76.9	+++	41.0	Temp	−−−	70.9	NS	NS	TIN		54.6	+++	76.3
	N:P	+++				Caddisfly	−−−				N:P	++			
	SRP	++									Temp			++	
	Temp	+++									Caddisfly	−−		−	
											Mayfly	−			
Algal cell density	TIN	−−	83.5	+	41.8	Midge	−	28.3	NS	NS	TIN		54.8	+++	66.8
	N:P	+++		+++							N:P	++			
	Temp	+++									Temp			+	
	Caddisfly	+									Caddisfly	−			
											Mayfly	−			
% live diatoms	TIN	−−−	79.9		45.4	N:P	+	26.3	++	50.4	TIN	NS	NS	++	76.5
	N:P	++		+++		Temp			++		N:P			+++	
	Caddisfly	+				Caddisfly			+		SRP			+++	
	Midge	++									Temp			+++	
	Mayfly	−													
DCA axis 1	N:P	++	42.2	NS	NS	TIN	+	72.9	+	83.0	TIN	NS	NS	+	22.3
	Mayfly	+				N:P	−								
						SRP	−−−								
						Temp			++						
						Caddisfly			−−−						
DCA axis 2	TIN	−−	44.9	NS	NS	N:P	−−−	73.4	+++	70.0			NS	NS	
	SRP	+++				SRP									
						Temp			+++						

Densities of all three major groups of algivorous insects were also reduced significantly by melt discharge in 1995, but mayfly nymphs and chironomids recovered, whereas grazing caddisflies did not. Although more mobile taxa can seek refugia from abrupt discharge increases (Rempel et al. 1999) and return soon after recession, slow-moving, cased caddisfly larvae are susceptible to mortality during large floods (Wooton et al. 1996). Caddis larvae can, however, respond to changes in current velocity and move to in-stream refugia when exposed to more gradual discharge elevation (Poff and Ward 1992), as occurred during the protracted 1997 snowmelt. Thus, postmelt reductions in insect densities in 1997 were transient for all groups, likely arising from the return of invertebrates from refugia to cobble surfaces.

Spatial and temporal variation in the habitat template— Hydrology and streamwater nutrient concentration: Dissolved nitrogen levels in Rio Calaveras stream water exhibited distinct seasonal fluctuations (Valett unpubl. data). High concentrations occurred in winter, when N demand by soil microbiota and plants in the catchment was low, whereas low TIN was measured under summer conditions of higher biotic activity in aquatic and terrestrial systems (cf. Vitousek 1977). The extent of TIN retention in any given year relates to the timing and extent of soil freezing and melt initiation (Williams et al. 1996*a*). Nested within the pattern of general seasonal change in streamwater nitrogen content was significant smaller-scale variation, the magnitude of which was particularly large in the driest of our 3 yr of study. Gross seasonal differences in the strength, direction, and spatial variation in hydrologic exchange varied in a similar manner. Positive mean VHGs in the upstream reach existed in the summers of 1995 and 1997, following high and moderate snowmelts, respectively. Consistently negative mean VHGs occurred in both reaches during nearly all of the 1996 drought year (Valett unpubl. data).

Hydrologic responses to snowmelt varied between reaches, with upwelling conditions occurring far more often in the upstream reach, whereas downwelling conditions persisted downstream. At the same time, concentrations of TIN were consistently higher upstream than downstream because of elevated nitrogen inputs to the stream associated with influsion of hyporheic water. The general pattern of higher TIN during snowmelt periods, when upwelling conditions persisted (i.e., May–June 1995, 1997), and lower TIN during the summer months, when both reaches were downwelling zones, supports this interpretation. Accordingly, TIN concentrations were low throughout the spring melt period during the 1996 drought, when both reaches remained downwelling throughout the year. Baker et al. (2000) observed similar responses for in-stream dissolved organic carbon at Rio Calaveras, with increases during snowmelts of 1995 and 1997 but no evident increase during the 1996 melt. TIN within a reach on a given sampling date was characterized by a single measure. This may contribute to the substantial variation in TIN we observed within seasons. Valett et al. (1996) noted that patterns of hydrologic exchange and distribution of microbial consortia that control biogeochemical transformations at the surface-groundwater interface are heterogeneous at small spatial scales. Thus, chemical observa-

tions applied to our study reaches likely integrated the products of multiple biogeochemical pathways that varied in magnitude, creating spatial variation in stream-water chemistry (cf. Dent and Grimm 1999).

Heterogeneity in stream-water nutrient content can arise from a number of mechanisms. These include spatial variation in geology or land use within a catchment (Biggs 1995), variation in distribution of N_2-fixing microbiota (Grimm and Petrone 1997), and biotic assimilation downstream of areas of nutrient input (Mulholland and Rosemond 1992). The location, spatial extent, and hydrologic intensity of subsurface upwellings are also influential (Valett et al. 1994) and are sensitive to variation in stream discharge and groundwater recharge (Lee and Hynes 1977). Dent and Grimm (1999) reported that spatial heterogeneity in surface-water nitrate concentrations along 10 km of a Sonoran Desert stream increased over 9 months after a large winter flood. Furthermore, the strength of spatial dependence in nitrate content from stream water collected at sequential sites 25 m apart increased with successional time, whereas the distance at which this dependence was manifested decreased. Sites of nutrient input via groundwater upwelling became more localized with discharge reduction and with increases in assimilatory demand by benthic microbiota in the absence of scour disturbance. Valett et al. (1996) reported similar results for nitrate, with heterogeneity in surface and subsurface nitrate content in three montane headwater streams of differing catchment geology tied to variation in stream discharge and intensity of hydrologic interaction between surface and subsurface waters.

Our results suggest similar control of stream-water nutrient content in Rio Calaveras. Groundwater recharge after the extremely low snowmelt in 1996 was minimal. Zones of upwelling were uncommon and localized in our upstream study reach during postmelt discharge recession. Downstream areas received surface water primarily from upstream, with minimal shallow groundwater intrusions. Divergence in stream-water chemistry between study reaches occurred as upstream assimilation reduced the pool of dissolved N available for downstream transport. In contrast, snowpack was relatively heavy in 1995 and 1997, and spring melt induced groundwater recharge throughout the reach (Baker et al. 2000). Hill slope and floodplain inputs to the alluvial aquifer resulted in protracted groundwater discharge into the stream for a longer section of channel (cf. Wroblicky et al. 1998), reducing heterogeneity in nutrient supply to benthic biota. In 1995, when snowmelt was abrupt and of greatest magnitude, N : P ratios varied from values suggesting N-limitation during snowmelt and late summer to values reflecting potential P limitation in midsummer, with similar temporal variation in N : P ratios in both study reaches. Patterns of temporal change in N : P ratios in 1997 also behaved similarly between reaches, but N : P declined steadily throughout postmelt recession, indicative of increasing N limitation. In summary, the timing and intensity of freezing and snowmelt (Williams et al. 1996*a*) and biogeochemical processing within the hyporheic zone (Valett et al. 1996; Baker et al. 2000) likely accounted for the main differences in relative abundance of dissolved N and P observed among study years in Rio Calaveras.

Grazing macroinvertebrates: Microalgal assemblages were subjected to grazing pressure that differed in both intensity and quality during each year of our study, as a result of interannual variation in proximate and subsequent effects of snowmelt intensity. This is because aquatic macroinvertebrates differ in susceptibility to flow-related disturbance (Wooton et al. 1996) and also differ in their effect on spatial heterogeneity, biomass, and species composition of stream autotrophs. Among the groups well represented in Rio Calaveras, cased caddisfly larvae are typically more efficient at consuming algae than mayflies (Lamberti et al. 1987). These differences diminish, however, as mayfly densities increase (Colletti et al. 1987); mayflies also appear to be more efficient algal digestors (Peterson et al. 1998). Although less studied, significant reduction in microalgal densities by chironomid larvae have also been documented, particularly for large instars (Welton et al. 1991).

Interannual differences tied to year-to-year variation in stream discharge have been reported in macroinvertebrate assemblages from a number of lotic systems (e.g., Feminella and Resh 1990; Boulton et al. 1992). Feminella and Resh (1990) reported that the lack of significant disturbance-induced reductions during a drought year in densities of the algivorous caddisfly, *Helicopsyche borealis,* increased competition among larvae and decreased adult fecundity altering larval recruitment the following year. Such lag effects have been noted after drought years in macroinvertebrate assemblages in other streams (Boulton and Lake 1992). Similar biotic interactions or delayed colonization from flow refugia likely contributed to the changes we observed in macroinvertebrate densities.

Microalgal response to within- and among-year shifts in the habitat template—Our analyses show that algal dynamics were affected by suites of physical, chemical, and biological control factors that differed among years in number and identity, as well as in the degree, timing, and spatial extent of influence. Although distribution of algivorous macroinvertebrates is often explained reasonably well by distribution of their microalgal food (Poff and Ward 1992; Peterson et al. in press), the converse relationship is less robust (Rosemond 1994; Peterson et al. in press). This is because the rapid generation times of benthic microalgae make them sensitive to many environmental factors, only one of which is herbivory.

Snowmelt-induced reduction of grazer densities in 1995 provided a period of relatively low grazing pressure for benthic algal accrual. Studies of macroalgae in freshwater (Dudley and D'Antonio 1991) and marine (Harris et al. 1984) systems have shown that spatial refugia can provide a "head start" for primary producers, allowing them to pass through grazer-susceptible developmental stages relatively unexposed to herbivory. Laboratory stream experiments by DeNicola et al. (1990) showed that benthic microalgae can outgrow susceptibility to certain types of grazers if a "temporal refugium" allows enough grazer-free development time, a phenomenon demonstrated in natural systems by Power (1992). In our study, effects of algal release from grazing pressure were short-lived, apparently because algal

assemblages had not attained grazer-resistant physiognomy before recovery of mayfly and midge densities.

Differences between upstream and downstream reaches were noted for all algal response variables in 1996 and appeared to be related most strongly to midsummer divergence in N:P ratio. Prior to this, algal biomass appeared to be constrained by grazing, as suggested by consistently low diatom live-cell percentages in both reaches and negative grazer-related regression coefficients for many algal variables upstream. In the downstream reach, grazing pressure may have maintained low algal biomass, precluding detection of significant relationships between algae and variation in grazer densities. The dramatic increase in algal biovolume and shift in taxonomic structure in the upstream reach coupled to an increase in N:P ratio is consistent with predictions made by Stevenson (1997) that major changes in algal community attributes should coincide with transitions between thresholds delimiting dominant determinants of community structure—here reflecting transition from grazing control to nutrient control.

Nutrient-related changes in algal assemblages in the upstream reach in 1996 were primarily induced by proliferation of large-celled diatoms that are common early colonists of clean substrata or abundant in ungrazed, nitrogen-rich environments (Peterson et al. 1993; Stevenson and Pan 1996). These taxa also appear to be easily ingested by aquatic herbivores (Lamberti et al. 1987), more easily digested (Peterson and Boulton 1999), and more susceptible to invasive infection (Peterson et al. 1993) than other algal taxa. Thus, proliferations induced by transient increases in nitrogen from zones of hydrologic upwelling or increased runoff can translate to increased resource availability for primary consumers.

Algal taxonomic structure in 1997 changed little from April to July, in contrast to the first 2 yr of our study, and biomass declined steadily. At the same time, herbivore densities were higher than those in preceding years and increased throughout melt recession. N:P ratios were indicative of probable N limitation throughout the 1997 melt and postmelt record. Epilithic algal assemblages were dominated by adnate, ingestion-resistant diatoms (Colletti et al. 1987) and small, chain-forming *Fragilaria* that are readily ingested but are more difficult to digest (Peterson et al. 1998). A precipitous decline in diatom live-cell percentages also coincided with increased grazer densities. These results indicate strong top-down (sensu Carpenter et al. 1985) control on algal assemblages in 1997.

Concluding remarks—Hunter and Price (1992) present a compelling case for viewing the dynamics of ecological communities in the context of a "bottom-up" template, the attributes of which shift in space and time to reflect heterogeneity in abiotic control factors. Our results illustrate that the initial structure of the habitat template for benthic algae, and its patterns of spatial and temporal change, are strongly influenced by the intensity and timing of snowmelt in Rio Calaveras.

Effects of physical disturbance on ecological communities are typically assessed in terms of biotic resistance and patterns of subsequent recovery (e.g., Holling 1973). Although the degree of biotic resistance exerted some influence on

postmelt biomass, taxonomic structure, and patterns of spatial heterogeneity in algal assemblages, these attributes were affected predominantly by temporal changes in nutrient supply set in place by hydrologic variation induced by snowmelt. Coinciding with these nutrient influences, and at times overriding them, were effects of grazing pressure. When snowmelt did not reduce populations of grazing macroinvertebrates and nitrate availability was high, top-down factors often were dominant controls of benthic algal dynamics. The severity of flow-related disturbance in stream systems that experience seasonal precipitation cycles is often dependent on broad-scale variation in global weather patterns (Molles and Dahm 1990). Although the proximate effects of such seasonal events vary predictably with disturbance intensity, subsequent changes in the habitat template, set in motion by initial disturbance effects, exert more long-term influence on community dynamics and are critical to understanding biological variation within stream ecosystems.

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