Flood disturbance, algal productivity, and interannual variation in food chain length

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The length of a river food chain changed from year to year, shifting with the hydrologic regime. During drought years, grazers suppressed algae across a nutrient gradient, while predators were functionally unimportant. Following flood disturbance, predators suppressed grazers, releasing algae. These results suggest that hydrologic regime, rather than productivity, determines the functional length of this river food chain. Within years, algae and grazer biomass responded to an experimental productivity gradient in patterns predicted by simple trophic models that assume efficient energy transfer. Understanding differences among species within trophic levels, however, was crucial in delineating the controlling interactions.

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A central challenge in ecology is to determine when simple, general models can explain patterns in nature, and when more details about species and environments are needed. Food chain models that predict changes in trophic structure across productivity gradients address this issue, because simple models and models that incorporate more natural complexity make different predictions (e.g. Fretwell 1977 vs Arditi and Ginzburg 1989; Fig. 1). The simplest models of trophic interactions assume closed systems, efficient energy transfer from resources to consumers, and consumers that track their resources closely through space and time and do not interfere with each other (Fretwell 1977, Oksanen et al. 1981). Under these conditions, consumers, if not suppressed by their own predators, can flatten biomass accrual of their resource across productivity gradients. These simple models predict that the biomass of the top trophic level, and of trophic levels even numbers of steps below it will increase with productivity, while biomass in remaining trophic levels will not increase (Fretwell 1977, Oksanen et al. 1981; Fig. 1A). Further-

thermore, simple models predict that food chain length increases with primary productivity. Here, food chain length is defined as "the number of trophic levels that are alternately released and suppressed following the removal of a top predator, with the criterion that changes in biomass at higher trophic levels must affect biomass of primary producers." (Power et al. 1996). We use this functional definition of food chains, which requires population regulation of lower trophic levels, because it is necessary to test models of food chain dynamics, in contrast to food chains defined by descriptions of energy transfers inferred from diet studies (Persson et al. 1996). Because the original models assume equilibrium densities of all trophic levels, tests required that experiments run long enough for all trophic levels to reach equilibrial biomass. A subsequent model, which assumed shorter time scales and behavioral responses of higher trophic levels to resources, also predicted that in food chains with efficient consumers, top predators could flatten biomasses of their resources across productivity (Wootton and Power 1993).

More complex models include factors that reduce the ability of consumers to harvest or suppress their resources. Oksanen et al. (1981) consider the case in which herbivores, at higher ranges of environmental productivity, can no longer convert all of the plant production to their offspring. In this case of herbivore satiation, plants but not predators are predicted to increase with further increases in productivity, causing increased input into the detritus food web. This lack of predator response is also predicted in ecosystems with low energetic efficiency. A linear increase in the third or fourth trophic level is only predicted in systems with high energetic efficiency in which the dominant species in the second or third trophic levels have high turnover rates and a high physiological capacity to convert resources to predators (Oksanen et al. 1981). Third or fourth trophic level carnivores in food webs dominated by ectotherms (with relatively high energy efficiencies) should respond linearly to increases in productivity because they are able to transfer increases in productivity to higher trophic levels. By contrast, carnivore responses to increases in productivity in endotherm-dominated food webs are constrained because a high proportion of their energy is diverted to heat production rather than reproduction. Ectotherm food chains are thus predicted to be longer than endotherm food chains.

Other models incorporate even more complexity, such as import of resources from outside the system, interference among consumers, ontogenetic changes in consumers' diets, imperfect tracking by consumers of spatially heterogeneous resources, and invulnerability of some resource organisms to predation. These more complex models predict that biomass in all trophic levels will increase with ecosystem productivity (Getz 1984, Mittelbach et al. 1988, Arditi and Ginzburg 1989, Leibold 1989, Oksanen et al. 1995, Nisbet et al. 1997, Fig. 1B). Both simple and complex models both assume that food chain length is constant.

Legend:
— 1 Level Food Chain - Algae
– – – 2 Level Food Chain - Algae + Grazers
·········· 3 Level Food Chain - Algae + Grazers + Predators
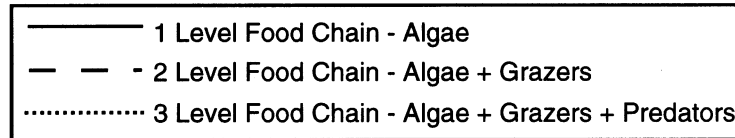
A. Predictions for Energy Efficient Models

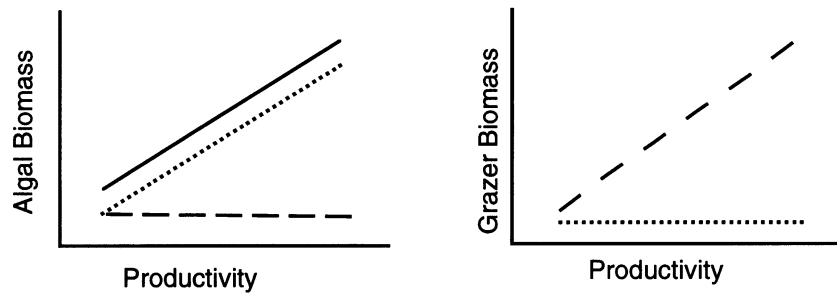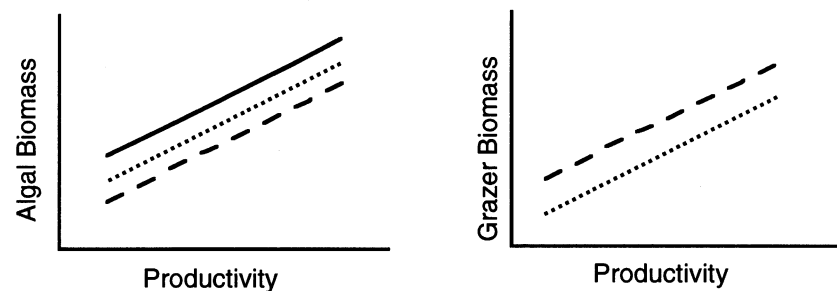## B. Predictions for Energy Inefficient Models

Fig. 1. Contrasting predictions of simple energy efficient models and more complex energy inefficient models of algal and grazer responses to productivity gradients in one, two, and three level food chains. Energy efficient models predict that biomass of top trophic levels and of trophic levels even number of steps below it will increase linearly with productivity while biomass in remaining trophic levels will not increase; in contrast energy inefficient models predict positive correlations of all trophic levels with productivity regardless of the length of the food web.

To examine whether simple models were adequate to characterize a river food chain's response to productivity, we manipulated nutrient availability to river algae during three consecutive summers in a river in northern California. Nutrient manipulations were crossed with trophic manipulations (grazer and predator exclosures) to better understand the mechanisms behind algal and grazer responses to productivity. Interannual comparisons of algal and grazer responses to experimental manipulations were used to test for interannual variability in food chain length.

Methods

Site description

Our experiments were conducted in the South Fork of the Eel River in Mendocino County, California (39°44'N 123°39'W). The region has a mediterranean climate, with most rain falling between October and April. During the dry summer months, the river becomes a series of large, lentic pools (1–4 m maximum depth), connected by riffles and shallow runs. We installed our experiments along the shallow margin of a run, in water approximately 0.2 m deep. Larger fishes, which play strong roles in deeper habitats of the South Fork Eel River (Power 1990, 1992), did not occur in these shallows, where the major components of the food web were algae (primarily diatoms), grazing insects (mayflies and midges) and snails, and predatory invertebrates (odonate larvae, primarily lestid damselfly nymphs, *Archilestes californica*) and small fish (three-spined sticklebacks, *Gasterosteus aculeatus*). The site received approximately 8 h of direct sunlight per day in summer. Dissolved nutrient concentrations in the South Fork Eel were sufficiently low to limit algal productivity (NO$_3$-N 8.0 μg L^{-1}, soluble reactive phosphorus 1.1 μg L^{-1}).

The first two years of the study (1991 and 1992) were drought years, during which the river did not experience any scouring floods. The drought ended in 1993, when high winter discharges scoured the river bed before the summer experiments. The largest discharges in 1991 and 1992 were 55 and 31 m^3 s^{-1}, respectively. Both occurred in March and were well below bankfull. During these years, discharge dropped to well below 1 m^3 s^{-1} by April, and continued dropping steadily through the spring and summer. In the winter of 1993, flood discharges of up to 376 m^3 s^{-1} (well above bankfull) occurred, and high base flows were maintained into the summer by an unusual late May-early June flood with a peak discharge of 142 m^3 s^{-1}. In 1991 and 1992, experiments were conducted in July; in 1993, experiments were conducted in August when flow rates and river depth were comparable to the experimental period during previous summers.

Experiments

To manipulate nutrient availability, we used nutrient diffusing clay flower pots filled with various concentrations of NaNO$_3$ and NaPO$_4$ (Fairchild and Lowe 1984). In 1991, we used four nutrient concentrations in addition to unenriched agar controls: 0.125 M N + 0.0125 M P; 0.25 M N + 0.025 M P; 0.5 M N + 0.05 M P; 1.0 M N + 0.1 M P). In 1992 and 1993, we used two nutrient concentrations in addition to agar controls: 0.25 M N and 0.025 M P; and 1.0 M N + 0.1 M P. We manipulated access of consumers to these flower pots by placing individual pots in buckets with large screened windows. Four screened windows, 25×25 cm^2, opened up about 75% the wall area of each plastic 12-L bucket. As anticipated, mayfly biomass was reduced by over 75% in buckets screened with the 0.3-mm mesh compared to the 1.0-mm mesh buckets. The 0.3-mm mesh buckets excluded most macroinvertebrates, with the exception of some small midges, but high algal accrual on pots in these treatments suggested that these small grazers had small effects. Buckets with 1.0-mm mesh windows were colonized by mayflies and larger midge larvae, and total grazer biomass on these substrates was significantly higher than in buckets with 0.3-mm mesh ($F = 12.48$, d.f. = 1,21, $p < 0.002$). Buckets with 0.3-mm mesh windows were used for the 'algae, one trophic level' treatment; buckets with 1.0-mm mesh admitted mayflies and larger chironomids and were used for the 'algae + grazers, two trophic level' treatment. During all three years, we also placed nutrient-enriched and control pots outside buckets, in the open river. In 1993, we enclosed sticklebacks or lestid damselfly nymphs in 1.0-mm mesh buckets for 'algae + grazers + predators, three trophic level' treatments. Many of the lestids underwent their final larval molt and emerged over the course of our experiments. Undergoing metamorphosis reduced their per capita effectiveness as predators. In a second predator experiment in late August, we enclosed lestids at twice the density (4/enclosure) to compensate for emerging lestids. This high density lestid treatment was compared to sticklebacks at the original densities (2/enclosure). These predator enclosure treatments allowed us to measure impacts of predators at manipulated densities (26–52 m^{-2}) which fell within the range of natural field densities of odonates in shallow habitats (Power 1992), but did not allow us to examine predator tracking of prey in our buckets. We attempted to study predator tracking with buckets with 6-mm mesh windows, but these were not colonized by representative densities of small predators, possibly because odonates were unable to crawl up the 5.0-cm-high plastic walls to reach the screened windows.

After each experiment ran for 20–28 d, we harvested and quantified algal biomass as ash free dry mass (AFDM) and counted invertebrates (1993 only) under $10 \times$ magnification, using length–weight regressions to compute their biomass (Smock 1980). In 1991 and 1992, algae were harvested by placing pots in plastic bags underwater, and scraping algae from the entire (264 cm^2) pot surface. In 1993, we sampled both algae and invertebrates on portions of the flowerpots. To prevent loss of organisms, we enclosed the pot in a cylinder before removing it from the water. The cylinder was covered at the top by 0.3-mm mesh screening, and sealed at the base with a gasket held tightly against the plastic base glued onto the bottom of the flower pot. The pot in this cylinder was immediately transferred to a dissecting pan in the field. Subsamples of algae were scraped off of two 2.2-cm-wide $\times$ 8-cm-long strips. Invertebrates were removed from these samples and from the remaining pot surface and preserved in 70% ethanol for invertebrate counts. Algal samples were filtered onto Whatman glass fiber filters, dried for 24 h at 64°C, and weighed. Filters and algae were then combusted at 500°C for one hour and reweighed for computation, by subtraction of the ashed from the dry weight, of ash free dry mass. For invertebrate mass estimates, the lengths of at least 50 individuals of a taxon, or all individuals if the sample contained less than 50 individuals of that taxon, were measured. Masses were estimated from published taxon-specific mass–length regressions (Smock 1980). Midges and mayflies accounted for $> 98\%$ of the grazing insect numbers, with *Centroptilim* sp. accounting for $> 99.0\%$ of the mayflies. Midges were divided into Tanypodinae (predators) and all other tribes, which are grazer/detritivores (Merritt and Cummins 1984). Only grazer/detritivore midges were included in this analysis. Relative abundance of major algal taxa was determined by counting at least 200 cells from three randomly chosen replicates of each treatment. Biovolumes were estimated by measuring mean lengths and widths of approximately 50 cells of each taxon.

In 1993, after substrates were harvested, we sampled an agar plug from three randomly chosen substrates in the 0.3-mm, 1.0-mm and open-river treatments to test for differential flow effects on nutrient release rates. Agar cores were dried at 65°C, ground to a fine powder and analyzed by Dumas combustion on a Carlo-Erba CHN elemental analyzer for % nitrogen by weight.

We used two-way ANOVA to test for differences in response variables (algal and grazer biomass) among nutrient and trophic treatments. To evaluate the fit of our data to simple and more complex trophic models, we performed regression analyses to test for positive slopes of algal and grazer biomass across the experimental nutrient gradient.

Results

During all three years, algae in the 'one trophic level' treatments (0.3-mm mesh buckets) increased with nutrients, indicating that algae, when released from heavy grazing pressure, were nutrient limited during both drought and flood years, although the shallower slope of this response in 1993 suggests that algae were more nutrient limited during drought years than in the flood year (Fig. 2). ANOVA results reveal significant nutrient and trophic effects all years ($p < 0.05$) and significant interactions between nutrients and trophic treatments in 1991 and 1992. Algal biomass responses to nutrients in the presence of grazers were intermediate between predictions of the simple and more complex models, but their fit to predictions of the simpler models was generally better. In enclosures which admitted grazers, algal biomass increased, but only modestly, in 1991, somewhat more strongly during the second year of drought in 1992, and did not increase with nutrient level during the 1993 flood year (Fig. 2). The increase in algal biomass with nutrients in stickleback enclosures during 1993 demonstrates the predicted release of algae from herbivory by these predators (Fig. 2). Enclosed lestids also permitted algae to increase with nutrients, but had to be stocked at twice the density as sticklebacks to produce the same effect (Fig. 3).

In the open river, algal biomass accrual was low during the drought years, and was similar to accrual in the two trophic level enclosures, with modest (1991) or no (1992) increase in biomass with nutrient enrichment (Fig. 2). In the flood year (1993), however, algae grown on pots in the open river increased with nutrients, closely resembling responses in the predator enclosure treatments (Fig. 2).

The response to productivity of one grazer guild, mayflies, corresponded well to predictions of the simpler trophic models. Mayfly biomass increased with nutrient level in the two-trophic level treatments, but not in predator enclosures or in the open river (Fig. 4a). In contrast, midges were not reduced by predators, nor were they positively correlated with nutrients in any of the trophic treatments (Fig. 4b). Total grazer biomass showed no clear pattern across the nutrient gradient because the weak and variable responses of midges masked the response of mayflies (Fig. 4c).

Algal species composition also shifted with trophic regimes and nutrient availability. Under reduced grazing pressure (in one-trophic level and three-trophic level enclosures, and in the open river during 1993), unenriched pots supported clouds of loosely attached diatoms (*Epithemia* spp. constituted approximately 70% of total algal biovolume), while about 65% of total algal biovolume on enriched pots was made up of filamentous green algae (*Stigeoclonium tenue, Spirogyra* sp., and *Ulothrix* spp.) and diatoms (*Melosira varians,* and *Nitzschia* spp.), taxa that can thrive with low
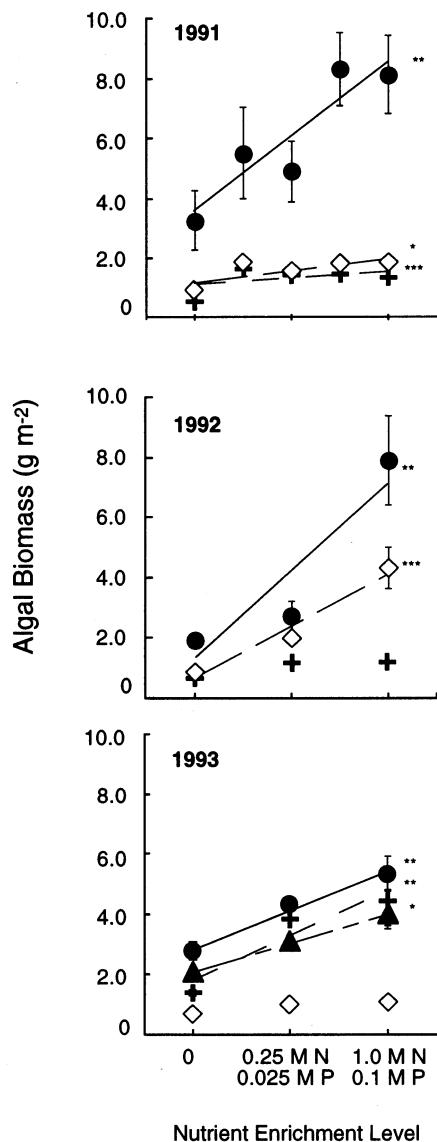
Fig. 2. Algal biomass (a.f.d.m. mean ± se), standardized by the length in days of the experiment) along the experimental productivity gradient for the summers of 1991 (drought year), 1992 (drought year), and 1993 (flood year) in one-level (●), two-level (◇), three-level (1993 only, ▲), and open river (+) trophic treatments. In 1991 and 1992, experiments were conducted in July; in 1993, due to unusually late spring floods, experiments were conducted in August when flow rates were comparable to the previous summers. ANOVA results reveal significant nutrient and trophic effects all years ($p < 0.05$) and significant interactions between nutrients and trophic treatments in 1991 and 1992. P-values for regressions are represented by $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$. Regression line is shown only when slope is significantly different from zero ($p < 0.05$).

grazing pressure (Steinman et al. 1987, Marks and Lowe 1989). When subjected to heavy grazing (in two-trophic level enclosures during all three years, and in the open river during the drought years), algae were

dominated by prostrate taxa, with 60% of algal biovolume comprising the diatoms *Achnanthes minutissima*, *Cocconeis* spp., and isolated cells of *Epithemia* spp. on unenriched substrates, while enriched substrates had a thin layer of green basal cells (e.g. basal pads of *Stigeoclonium tenue* were 62% of total algal biovolume), which are difficult to graze because they adhere tightly to the substrate and secrete slippery mucus (Lamberti et al. 1987, Marks and Lowe 1989). Species composition within trophic treatments was similar all three years with the exception of the open river substrates, which had prostrate taxa in drought years and filamentous and loosely attached taxa following the flood year (Marks 1995).

Artifactual effects of flow impedance, such as the reduction of algal growth by siltation or diminished light or nutrient fluxes, can be problems in screened stream enclosures, and tend to increase with smaller mesh sizes. Several observations suggest that flow effects in our enclosures were minor in comparison with effects of nutrient and trophic treatments. Different trophic treatments using the same 1.0-mm mesh size showed strong differences in algal accrual, depending on the presence or absence of predators, showing that algal accrual was not a function of mesh size (Fig. 2).
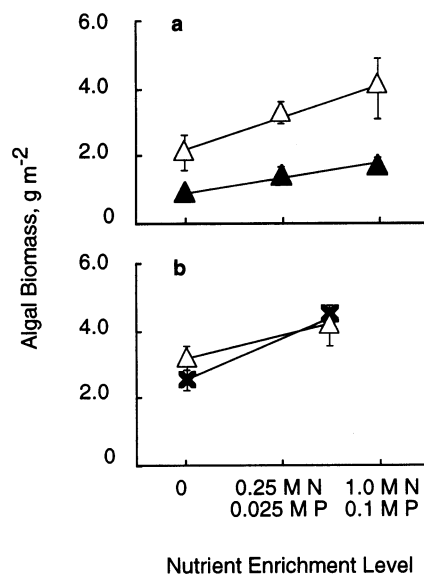

Fig. 3. Algal biomass (mean ± se) as affected by the presence of stickleback predators (△) and lestids predators at low (▲, a) and high densities (×, b), showing that lestids cause a similar trophic cascade as sticklebacks at high densities (b) but not at low densities (a). Low and high lestid densities began at two per enclosure and four per enclosure respectively, but because lestids emerged throughout the experiments we were not able to maintain constant densities. We replaced them every two to three days and estimate that actual densities on the low and high lestid density treatments were 1–2 lestids per enclosure and 2–4 lestids per enclosure respectively. Stickleback densities were two sticklebacks per enclosure in both experiments.
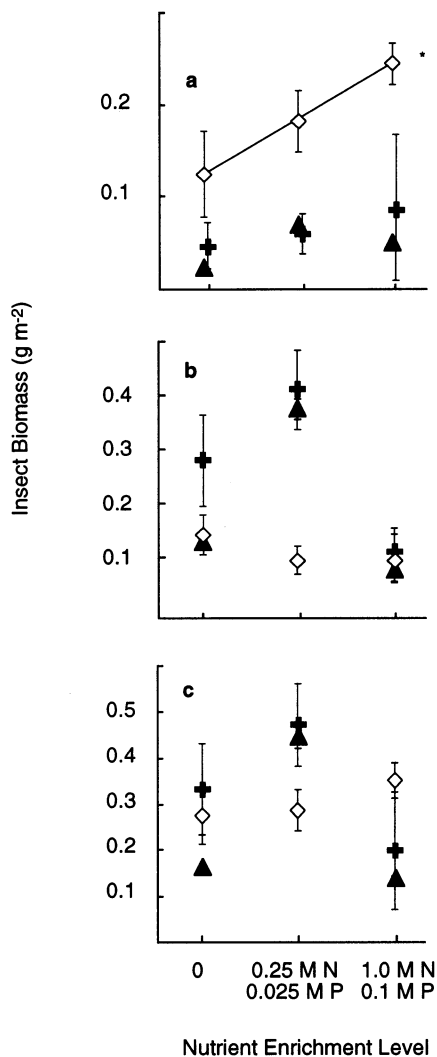
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Fig. 4. Biomass of (a) mayflies, (b) midges, and (c) total grazers along the experimental productivity gradient in 1993 for the two-level (◇), three-level (▲), and open river (+) trophic treatments shows that mayfly patterns followed the stepped accrual patterns predicted by the energy efficient model (Fig. 2), whereas midges and total grazers did not show clear patterns. Values are means ± se. Regression line is shown only when slope is significantly different from zero ($p < 0.05$).

Algal biomass accrual was similar in 0.3-mm mesh buckets and in 1.0-mm mesh buckets when these enclosed predators that reduced grazer abundance (Fig. 2: 1993), with slightly more accrual in the 0.3-mm mesh treatment. If flow reduction had been important, algal accrual would have been lowest in the smallest-meshed treatment. Pots in the open river experiencing unimpeded flow had the least algal accrual during 1991 and 1992, and higher levels, comparable to those in 0.3-mm grazer exclusion buckets, in 1993 (Fig. 2). Finally, there were no differential flow effects of mesh-size treatments on nitrogen concentrations in flower pots that had been incubated for 20 d in 0.3-mm and 1.0-mm mesh buck-

ets, and in the open river ($F = 1.130$, d.f. 2,11, $p = 0.358$).

Discussion

Algal responses to experimental manipulations show patterns more similar to the simple models that predict increases in biomass across nutrient gradients in one and three level food chains but not in two level food chains. Despite differences among algal taxa in food quality and vulnerability to grazing, the collective biomass responses of algae to nutrients were largely suppressed by grazers in two-trophic level enclosures in 1991 and 1993, and partially suppressed in 1992, as predicted by the simple trophic models (Oksanen et al. 1981 if grazers are unsatiated, Fretwell 1977). In contrast, the response of total grazer biomass followed no clear pattern because the two most abundant grazers responded differently. Despite this natural complexity, the influence of productivity on trophic level biomass in this river-margin food web could be fairly well predicted by the simple models, when responses by the key herbivore guild, mayflies, were distinguished. In three-trophic level enclosures, mayfly biomass, but not total grazer biomass, also responded as predicted by the simpler theories.

These results show that within a designated trophic level, some species have stronger effects than others on food web structure. Mayflies were better able to track spatial variation in their algal foods than midges. Midges in our experiments built retreats, attached to substrates, out of detritus and algal fragments which protected midges against predators (Hershey 1987, Power et al. 1992), but greatly restricted mobility. Therefore, mayflies were both more able to track and suppress algae, and more likely to transfer this energy to predators, meeting the assumptions of the simpler trophic models about consumers that mediate major channels of energy flow through food webs (Fretwell 1977, Oksanen et al. 1981). Midges, in contrast, by investing in defense, potentially reduce their feeding efficiency and reproductive rates, thereby reducing the rate at which they transfer energy to predators. Predatory sticklebacks had stronger per-capita effects on mayflies than lestids, probably due to their larger size and to the metamorphosis and emergence of lestid damselflies during our experiments (Fig. 3). Although algal species also responded differently to experimental manipulations, no individual species response strongly violated the assumptions of the simple models. Large quantities of 'inedible' algae never accumulated on the highly grazed substrates, in contrast to the predictions of Leibold (1989). Highly grazed treatments were dominated by 'grazer resistant' taxa that avoid grazing pressure via their prostrate growth forms. A trade-off

of this growth form is an inability to develop large biomasses, in contrast to the filamentous green algae, diatom chains, and clouds of *Epithemia* that formed on ungrazed substrate.

Differences between drought and flood years in nutrient effects on algal accrual in the open river suggested, however, that hydrologic rather than productivity regimes determined food chain length in this system. Although they were nutrient-limited all three years, algae on pots placed in the open river responded more strongly to nutrient enrichment during the flood year (1993, Fig. 2). The algal response in 1993 was not due to sparser grazer densities in the open river. Grazers in 1993 colonized predator exclusion buckets in sufficient densities to suppress algae (Fig. 2), indicating that the open river treatments experienced a three-level, rather than a one-level trophic regime. We offer two hypotheses for why the food chain may have lengthened from two levels in the drought years to the three levels in the flood year: 1) predator densities were higher during the flood year; 2) grazer guilds were more vulnerable to predators following flood disturbance. We favor the first hypothesis (increased predator densities) for this shallow river run. Higher summer base flows in 1993 maintained off-river pools and shallow marginal habitats which are refuges for odonates and small fish from larger, predatory fish that are restricted to deeper river habitats. Lestids in particular were more locally abundant in 1993 than in 1991 or 1992 (Marks 1995). The second hypothesis has been supported by surveys and experiments in deeper channel habitats of the South Fork Eel and other rivers, where densities of the large, heavily armored caddisfly, *Dicosmoecus gilivipes*, increase by 1-2 orders of magnitude during drought or in artificially regulated channels where scouring floods are eliminated (Power et al. 1996, Wootton et al. 1996). *D. gilivipes* densities were low during all three years in the shallow run where our nutrient experiments were conducted, and unlikely to have an effect in this part of the river. The only abundant armored grazers were small snails (*Physella gyrinus*), which had only weak (1993) or no (1992) effects on algae in this habitat (Marks 1995). Studies of food chain length in phytotelmata (water filled plant bodies) also suggested that disturbance rather than productivity determined food chain length (Kitching and Pimm 1985, Pimm and Kitching 1987); however, in contrast to our results, disturbance decreased rather than increased food chain length. In these systems, experimental disturbances reset species densities to zero, and food chain length was determined by rates of colonization of higher trophic levels. In the Eel River, flood disturbance during winter months does not eliminate insects and small fish predators during the summer low flow period when their densities are highest. These predators colonize the river every year but their densities are likely to vary significantly interannually, in part due to flow regime. In addition, the phytotelmata studies used descriptive trophic levels rather than functional levels making it difficult to compare the dynamics between the two sets of studies.

Our study shows that functional food chain length is not constant in the Eel River, but can vary over time, as well as over space (Power 1990, 1992). Results from these small-scale manipulations can only be extrapolated to the shallow runs in which they were conducted. Functional food chain length differs in other habitat types in the river (pools and deeper channels) where larger fish and grazers are present. Responses to trophic manipulations in these habitats have also differed interannually (Power 1992, Power et al. 1996). Interannual variation in the hydrologic regimes of rivers can alter the impacts of taxa at different trophic levels, offering periodic temporal refuges for prey, and contributing to the long-term maintenance of species diversity (Sparks 1992, 1995).

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