

# Productivity, consumers, and the structure of a river food chain

(predation/herbivory/multitrophic level theory/community ecology/predator-prey theory)

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**ABSTRACT** We tested models of food chain dynamics in experimentally manipulated channels within a natural river. As light levels increased, primary productivity and the biomass of algae and primary predators increased, but the biomass of grazers remained relatively constant. In the presence of a fourth trophic level, algae and primary predators decreased, but grazers increased. These results match predictions of food chain models based on classical predator-prey theory and suggest that simple models of multitrophic level interactions are sometimes sufficient to predict the responses of natural communities to changes in environmental productivity and predators.

Ecologists seek to describe the dynamics of natural systems and to predict responses of these systems to environmental change. Although ecological theory examining the dynamics of species competing for a common resource at one trophic level has been well developed (1–5), field experiments indicate that interactions among species at different trophic levels must be considered to predict the dynamics of natural communities (6–8). Models of food chains provide a first step in developing a theory of multitrophic level communities and represent an opportunity to link investigations at community and ecosystem levels. Therefore it is important to determine how well food chain models can predict changes in the dynamics of natural systems. Here we report results from a field experiment designed to test basic food chain models by examining the response of food chain structure to manipulations of primary productivity and secondary predators in a northern California river community.

Models of food chains are generally developed as extensions of basic predator-prey theory, which traditionally has assumed that the consumption rate of predators is a simple function of prey density (1, 2, 9–18). These models predict that community structure will be controlled by predators at the top and by plant productivity at the bottom of the food chain (9–18). In a food chain of a given length, increasing productivity is expected to increase the abundance of populations at the top trophic level and populations at alternate levels below it. Intervening trophic levels are not expected to increase in biomass with increases in productivity but experience faster turnover as the trophic level above crops the surplus productivity. For example, in a four-level food chain, increasing productivity should increase the abundance of secondary predators (i.e., consumers of primary predators) and herbivores but not primary predators (i.e., consumers of herbivores) or producers. In a three-level food chain, however, increasing productivity should increase the abundance of primary predators and producers but not herbivores. The models also predict that when the top consumer in the food chain is reduced or removed, abundances should alternately increase and decrease at sequentially lower trophic levels, producing a “trophic cascade” (12, 19–28).

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## METHODS

Tests of food chain models require the experimental manipulation of productivity while holding food chain length and community membership constant (29, 30). We conducted such a study in the South Fork Eel River on the Northern California Coast Range Preserve (34°44' N, 123°39' W) in Mendocino County, CA. We subdivided sections of a relatively homogeneous pool within the river to make 25 in-stream channels. We built channels (3.0 m long × 0.7 m wide × 1.5 m high) in blocks of five with frames of polyvinyl chloride pipe and wood that supported side walls of heavy black plastic and end walls of 6.0-mm plastic mesh. Mesh ends permitted water exchange (current in pool < 0.3 cm s<sup>-1</sup>) and access for algae, invertebrates, and small, but not large (>30 mm long), fish. Thus, food webs assembling inside channels were limited to three trophic levels. Walls were buried in the natural stream bed (stones 2–10 cm in diameter). We placed a set of four 7.5 cm × 7.5 cm ceramic floor tiles at the upstream and downstream ends of each channel to serve as uniform sampling substrates for algae and benthic invertebrates. We also placed tiles in the two 3.0 m × 0.7 m areas flanking each block of channels to determine how abundance patterns changed in areas accessible to a fourth trophic level (fish > 30 mm in total length).

We manipulated productivity in the channels by using roofs made of different materials: (i) clear plastic (mean photon flux density of photosynthetically active radiation,  $\bar{X} = 1342 \pm 36 \mu\text{mol of photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ,  $n = 5$ ), (ii) window screen ( $\bar{X} = 912.2 \pm 50.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), (iii) light shade cloth ( $\bar{X} = 582.7 \pm 43.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), (iv) heavy shade cloth ( $\bar{X} = 493.7 \pm 14.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and (v) black plastic ( $\bar{X} = 1.94 \pm 1.25 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Without roofs, light levels on the river bed under 40–60 cm of water averaged  $1514 \pm 90$  ( $n = 10$ )  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Each shade treatment was replicated five times and was assigned to channels in a randomized block design stratified to ensure that each treatment was represented in each of the five positions possible within a block.

We first conducted an experiment to verify that the different light regimes did not affect the foraging success of visual predators by introducing three (48–58 mm) preweighed steelhead (*Oncorhynchus mykiss*) into each of the 25 channels for 11 days and determining if light affected fish growth and survivorship. After removing all of the steelhead and measuring their wet weight, we initiated food web assembly experiments on 6 July 1991. We censused the channels after 30 and 55 days by visually counting fish and predatory invertebrates within each channel, by enumerating all small invertebrates on the top and bottom of each tile, and by scraping algae from two tiles per channel for taxonomic identification and ash-free dry weight analysis in the laboratory. Invertebrate and fish abundances were converted to biomass by collecting a sample of each taxa and determining its average dry weight.

Fifty-eight days into the experiment, we measured primary productivity in three replicates of each light treatment and

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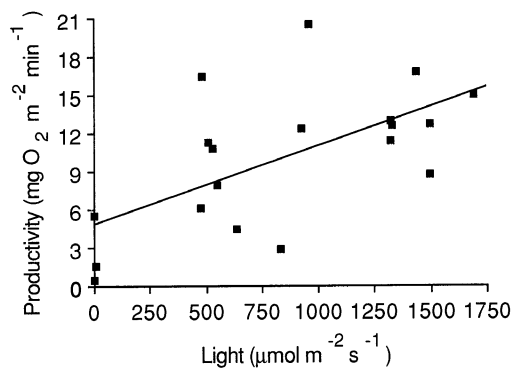


FIG. 1. Relationship between manipulated light level and gross productivity of algae in channels. Line of best fit: Productivity ( $\text{mg of O}_2 \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ ) =  $4.83 + 0.006 \text{ light } (\mu\text{mol of photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$ ,  $r^2 = 0.377$ ,  $n = 19$ . Light levels vary within treatments because of differences in water depth.

four areas outside the channels by placing a tile from each site tested into a sealed glass container filled with partially deoxygenated water (5.0 mg of  $\text{O}_2$ /liter) and returning it to its channel for incubation. Using a portable oxygen meter, we first measured depletion of  $\text{O}_2$  from respiration in complete darkness by wrapping the containers in aluminum foil for 1.5 hr and then removed the foil to measure net productivity in the channels after another 1.5 hr.

## RESULTS

Food chain models predicted the results of our productivity manipulations. As our experimental design intended, increas-

ing light levels increased productivity (Fig. 1, linear regression,  $P < 0.006$ ) but did not affect survivorship ( $\chi^2_4 = 6.18$ ,  $P > 0.1$ ) or growth (ANCOVA with number of survivors,  $F_{15}^4 = 1.37$ ,  $P > 0.25$ ) of steelhead in the channels during the preliminary feeding experiment. At both sampling dates, the biomass of primary producers (comprised primarily by the macroalgal chlorophyte *Cladophora glomerata* and its epiphytic diatom *Epithemia* sp.) correlated positively with light (Fig. 2 A and B; both  $P < 0.0001$ ). Likewise, the biomass of small predators (mostly three-spined sticklebacks *Gasterosteus aculeatus*, juvenile California roach *Hesperoleucas symmetricus*, damselflies *Archilestes californica*, and dragonflies *Aeshna californica*) increased with light on both sampling dates (Fig. 2 E and F; both  $P < 0.001$ ). In contrast, herbivore abundance showed no significant trends with light-limited productivity (Fig. 2 C and D; both  $P > 0.15$ ). Major herbivores included mayfly nymphs (mostly *Paraleptophlebia* and *Centroptilum*), caddisfly larvae (*Gumaga*, *Mysticides*, and *Lepidostoma*), snails (*Physella*), freshwater limpets (*Ferrissia*), midge larvae (chironomidae), and water pennies (*Eubrianix*). The slopes of the relationships between biomass and light within each trophic level did not differ significantly between the 30- and 55-day sample dates (ANCOVA testing interaction between sample date and light, all  $F_{46}^1 < 2.55$ ,  $P > 0.1$ ), suggesting convergence toward a stable pattern. The mean biomass of primary predators and algae declined slightly but significantly between sample dates, however, whereas the mean biomass of herbivores increased slightly (Fig. 2, ANCOVA, all  $F_{47}^1 > 4.47$ ,  $P < 0.04$ ), indicating that the system was not strictly at equilibrium. The alternating

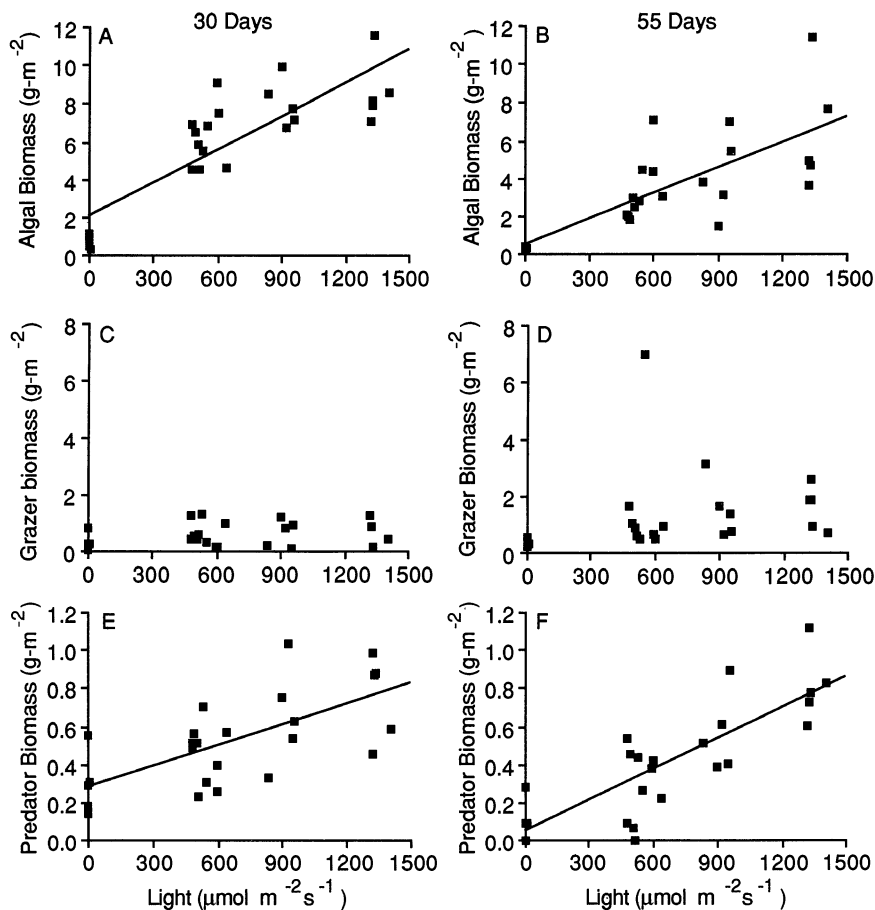


FIG. 2. Relationship between manipulated light level and biomass at each of the three trophic levels present within the channels. Statistically significant ( $P < 0.05$ ) lines of best fit from least-squares regression are shown ( $n = 25$ ). (A) Thirty-day algal biomass ( $A = 2.1 + 0.006 L$ ,  $r^2 = 0.713$ ). (B) Fifty-five-day algal biomass ( $A = 0.51 + 0.005 L$ ,  $r^2 = 0.574$ ). (C) Thirty-day grazer biomass ( $G = 0.42 + 0.0003 L$ ,  $r^2 = 0.082$ ). (D) Fifty-five-day grazer biomass ( $G = 0.81 + 0.0008 L$ ,  $r^2 = 0.062$ ). (E) Thirty-day predator biomass ( $P = 0.28 + 0.0004 L$ ,  $r^2 = 0.442$ ). (F) Fifty-five-day predator biomass ( $P = 0.05 + 0.0005 L$ ,  $r^2 = 0.676$ ).

increases and decreases of biomass at successive trophic levels were again as predicted by the models.

Changes in community structure with changing food chain length also followed predictions of the models. Areas outside the channels were exposed to large fish (steelhead, and adult roach), a fourth trophic level that feeds on small fish and predatory invertebrates, whereas these predators were excluded from inside channels (Fig. 3D). Both algal and small predator biomass outside the channels were 31% lower than in channels with clear roofs (Fig. 3A and C, one-tailed  $t$  tests,  $t_{11} = 2.90$  and  $2.24$ , respectively, both  $P < 0.03$ ), even though light levels were 13% higher. In contrast, herbivores were 48% higher in the presence of a fourth trophic level (Fig. 3B, one-tailed  $t$  test,  $t_{11} = -1.83$ ,  $P < 0.05$ ). These results suggest that large fish reduced the abundance of primary predators, which reduced predation on herbivores. Herbivores responded by increasing in abundance and exerted increased grazing pressure on algae.

### DISCUSSION

Simple food chain models successfully predicted the qualitative responses of our river community to changes in productivity (Fig. 2) and food chain length (Fig. 3). These models may apply to a variety of terrestrial, freshwater, and marine com-

munities that exhibit trophic cascades in response to the removal of a top predator (19–28). Some situations, however, will require the application of expanded models that account for differential susceptibilities of prey to consumers, changes in trophic architecture, spatial heterogeneity, ontogenetic diet shifts, omnivory, inter- and intraspecific interference, or differences in the time scales of mortality and recruitment processes (29–37). Any of these factors may cause abundances at different trophic levels to deviate from patterns predicted by the simpler food chain models. The alternative pattern predicted by many expanded food chain models, positive relationships among all trophic levels, has been reported in several observational studies comparing different communities (29, 30, 35). However, the relationship between productivity and trophic level biomass must be studied in experimental contexts with known, fixed numbers of functionally important trophic levels in order to evaluate the applicability of simple versus expanded food chain models to different communities (29, 30).

The predictions of food chain models are based on steady-state assumptions. Although no real system is likely to be strictly at equilibrium because of environmental variation and complex dynamics, if such variability is not too strong relative to the strength of the attracting equilibrium, the system will reside in a portion of phase space near the equilibrium (38). Detecting shifts associated with changes in equilibrium points requires experiments carried out over sufficiently long periods for the system dynamics to respond to the change. Several features of our experimental system enhance the speed of response to changes in parameters. First, life histories of freshwater organisms are generally completed much more rapidly than those of other organisms, leading to faster dynamics. Second, by evaluating biomass rather than abundance, we can account for changes due to storage and growth, as well as reproduction, which places the dynamics of all trophic levels on more similar time scales. Third, our experiments were affected by behavioral as well as demographic processes, because the channel ends allowed some exchange of predators and grazers with the outside river. Behavioral responses can have substantial effects on the dynamics of species interactions (39) and may be as critical as demographic responses to predicting qualitative changes in ecological systems. Because variation in demographic rates affects the evolution of habitat selection, rates of immigration and emigration should be related to habitat-specific demographic rates (in the absence of interference). Indeed, models of our system incorporating a mixture of behavior and demography predict the same changes as those based on pure demographic models (*Appendix*).

Food chain models are simple steps toward predicting the responses of ecological systems to change. In the future, more detailed models will have to be applied to predict the direct and indirect consequences of perturbations to particular species rather than to whole trophic levels (40). For example, experiments in lake mesocosms have demonstrated a variety of taxon-specific responses of plankton to manipulation of trophic architecture and nutrients (41–43). In some cases, taxon-specific differences in the susceptibility of prey to predators at different trophic levels can produce chain-like dynamics even in food webs with omnivores (24, 44). In our study, variation in the foraging efficiencies of predators on different prey also contributes to cascade dynamics. Juvenile California roach consume algae and grazing invertebrates and, as adults, predatory invertebrates too. Nevertheless, when we account for changes in diet by assigning different ontogenetic stages to different trophic levels, the Eel River community behaves like a food chain because the per capita impact of consumers on prey at different trophic levels varies (e.g., juvenile roach have stronger effects on algalivorous insects than on algae). Our results demonstrate that food chain models can successfully predict qualitative patterns of community response to changes in productivity and food chain length in our

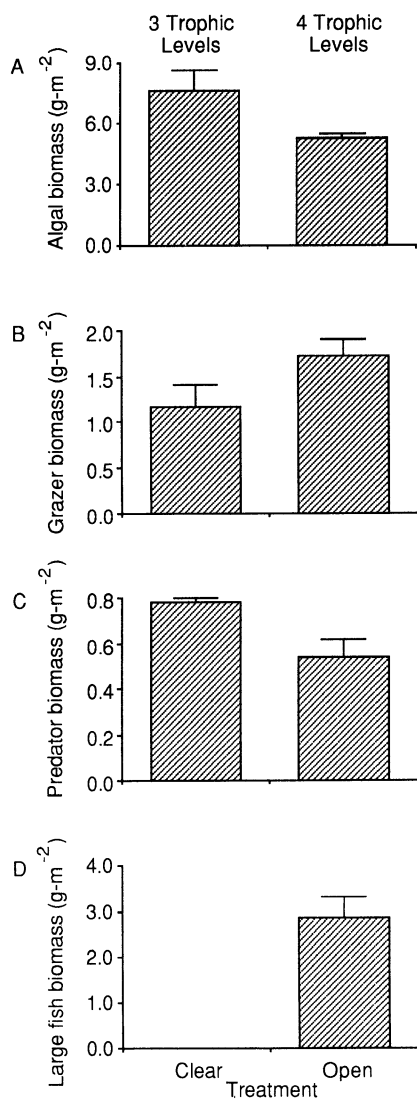


FIG. 3. Mean biomass ( $\pm 1$  SE) of different trophic levels in the clear channel treatment (no large fish,  $n = 5$ ) and outside channel treatment (large fish present,  $n = 10$ ), averaged over the 30- and 55-day samples. (A) Algal biomass. (B) Grazer biomass. (C) Primary predator biomass. (D) Secondary predator (large fish) biomass.

natural system. More detailed models accounting for interactions among multiple trophic levels are a promising avenue for interchange between theoretical and empirical ecologists.

#### APPENDIX: A food chain model containing a mixture of behavioral and demographic responses

In our system, it is reasonable to assume that local growth and death determine vegetation dynamics. Furthermore, grazer dynamics are assumed to be a function (*i*) of local birth, growth, and death rates, (*ii*) of density-independent immigration rates, and (*iii*) of emigration rates that are based only on local birth, growth, and death rates, because the scale of the experiments is large relative to movements of grazers. Predators, however, are sufficiently mobile to compare growth and death rates between a channel and the outside river, and so their dynamics are assumed to be determined by behavior in which they choose the habitat that has a lower ratio of mortality rate ( $\mu$ ) to growth rate ( $g$ ), as suggested by Werner and Gilliam (45). Then, a simple food chain model is:

$$\begin{aligned} dV/dt &= b_v V f(V, R) - c_h V H - m_v V \\ dH/dt &= I H_o + [b_h c_h V H - c_p P H - m_h H] \\ &\quad - e [c_p P H + m_h H - b_h c_h V H] \\ dP/dt &= [\mu_o P_o] / [g_o P_o] - \mu P / g P \\ &= [m_{p,o} P_o] / [b_p c_p H_o P_o] - [m_p P] / [b_p c_p H P], \end{aligned}$$

where  $V$ ,  $H$ , and  $P$  are the biomass of vegetation, herbivores, and predators inside a channel, variables subscripted by  $o$  are those from the outside river,  $b_x$  represents the ability of trophic level  $x$  to convert resources into biomass,  $c_x$  is the per-capita consumption rate of consumer  $x$ ,  $m_x$  is a per-capita density-independent loss term of trophic level  $x$ ,  $I$  is the per-capita immigration rate of herbivores from outside to inside a channel, and  $e$  is the per-capita probability of herbivores emigrating from the channel, which increases with increasing mortality and decreases with increasing vegetation. The function  $f(V, R)$  describes per-capita resource acquisition by vegetation and is assumed to increase with resource levels ( $R$ ) but decrease with  $V$ . Solving for steady state ( $V^*$ ,  $H^*$ , and  $P^*$ ), one obtains:

$$\begin{aligned} f(V^*, R) &= m_v / b_v + [H_o c_h m_p] / [b_v m_{p,o}], \\ H^* &= H_o m_p / m_{p,o}, \\ P^* &= [V^*(1 + e) b_h c_h + (1 + e) m_h + I m_{p,o} / m_p] / (1 + e) c_p. \end{aligned}$$

Because the river outside the channels is much larger than within the channels,  $H_o$  is approximately constant. Therefore, 1)  $f(V^*, R)$  is a constant, so increasing  $R$  increases  $V^*$  and  $P^*$ , whereas increasing  $m_p$  (adding a fourth-level predator) decreases  $V^*$  and  $P^*$  and 2)  $H^*$  is a constant that increases with increasing  $m_p$ , but does not change with increasing  $R$ . Similar predictions obtain in a two-habitat model for smaller habitats where predators and grazers behaviorally select habitats following the  $\mu/g$  rule and where changes in abundance in one habitat affect the abundance in the other habitat (J.T.W., unpublished model).

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