

THE EFFECTS OF PREY HETEROGENEITY AND CONSUMER IDENTITY ON THE LIMITATION OF TROPHIC-LEVEL BIOMASS

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Abstract. The effects of prey heterogeneity and consumer identity on the strength of predator limitation of prey biomass were explored experimentally under controlled laboratory conditions. In this study, I utilized a model aquatic community composed of zooplankton as top predators, algae as prey, and nutrients as basal resources. To examine the effects of prey heterogeneity, I created a food chain initially composed of a single edible prey and a food web initially composed of a diverse assemblage of algae. These two prey treatments were then fully crossed with two predator treatments (a large-bodied zooplankter, *Daphnia pulex*, and a small-bodied species, *Ceriodaphnia quadrangula*), and two levels of productivity. Prey heterogeneity had clear effects on the ability of predators to limit overall prey biomass. In food chains, predators had strong negative effects on algae, and algal biomass exhibited a narrow response to enrichment. In contrast, predator limitation was weak in food webs with the consequence that predator and prey biomass both showed positive increases with productivity. The prey community in food webs also exhibited a striking increase in the relative abundance of large inedible algae with enrichment, in keeping with model predictions. These results indicate that prey heterogeneity can have substantial effects on predator–prey dynamics and trophic structure and can serve to shift systems from strong top-down control to ones in which prey are colimited by predators and resources. Comparisons between top predators showed that *Daphnia*, compared to *Ceriodaphnia*, more strongly limited the biomass of large algae in food webs at high productivity and total algal biomass in all nutrient-enriched treatments (both chains and webs). Thus, consumer identity and ecological context (productivity and heterogeneity of prey communities) may mediate the strength of zooplankton–algae interactions and the efficacy of trophic cascades.

Key words: algae; bottom-up control; *Ceriodaphnia*; *Daphnia*; food web dynamics; keystone predation; top-down control; zooplankton.

INTRODUCTION

Ecologists have frequently focused on patterns of trophic-level biomass to infer ecological processes from community organization (Fretwell 1987, Power 1992, Leibold et al. 1997). The underlying rationale for much of this research has been predicated on the assumption that natural patterns of biomass partitioning, when examined along gradients of productivity, can provide insight into the factors controlling or limiting trophic levels (Power 1992, Leibold et al. 1997). The long-standing top-down, bottom-up debate is commonly approached in this manner and frequently centered on the predictions of Oksanen et al. (1981; Fretwell 1987, Power 1992). Their mathematical treatment, hereafter referred to as EEH or the “exploitation ecosystems hypothesis” (Oksanen and Oksanen 2000), predicts that trophic-level biomass is exclusively top-down or bottom-up “controlled” (sensu Osenberg and Mittelbach 1996). For example, in a two-trophic-level system composed of plants and herbivores, EEH pre-

dicts that plants are top-down controlled via the numerical response of herbivores, and thus their total biomass shows no response to increasing potential productivity at equilibrium. In contrast, herbivores, themselves having no predators, are bottom-up controlled and therefore respond positively. Hence, the EEH model predicts that consumer and resource control alternates as one moves up a food chain resulting in a concomitant decoupling of biomass in adjacent trophic levels along gradients of productivity (see Mittelbach et al. 1988, Oksanen and Oksanen 2000).

While the general EEH pattern has received some empirical support (e.g., Wootton and Power 1993, Mazumder 1994, Kaunzinger and Morin 1998, Oksanen and Oksanen 2000), a growing body of evidence suggests that the biomasses of adjacent trophic levels often increase jointly as ecosystem productivity increases (e.g., McCauley and Kalff 1981, Hanson and Peters 1984, McNaughton et al. 1989, Ginzburg and Akcakaya 1992, Leibold et al. 1997). This pattern is particularly well documented in aquatic communities where zooplankton and phytoplankton biomasses are commonly positively correlated among lakes and ponds of varying nutrient enrichment (McCauley and Kalff 1981,

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McCauley et al. 1988, Leibold et al. 1997). This chasm between model prediction and natural pattern has engendered an exploration of potential mechanisms that can generate positive correlations between the biomass of adjacent trophic levels and productivity (McCauley et al. 1988, Mittelbach et al. 1988, Arditì and Ginzburg 1989, Abrams 1996). Recent interest has been directed towards the effects of prey heterogeneity and differential resource edibility. The abstraction of food chain interactions, as in EEH, implicitly assumes functional homogeneity of species within trophic levels. When models are extended to include within-trophic-level heterogeneity (i.e., food chains become food webs) the strength of predator-prey interactions weakens, EEH patterns dissolve, and positive correlations between adjacent trophic levels can be generated (Leibold 1989, 1996, Abrams 1993).

To base predictions within a theoretical framework, consider a food web composed of a single top predator, a number of middle prey, and a single basal resource. As shown by Leibold (1996), if trade-offs exist among prey in predator susceptibility and competitive ability for resources, a serial replacement of prey species will occur as productivity increases (i.e., as the supply of basal resources increases). At low productivity only the most efficient consumers of resources can persist. As productivity increases the more predator-resistant but poorer resource competitors can invade (the well known "keystone predator" effect, sensu Paine 1966; see also Levin et al. 1977, Vance 1978, Holt et al. 1994). The keystone predator model predicts positive correlations between top predator and prey biomass along gradients of productivity, but weaker correlations if productivity is sufficient to allow the invasion of a completely inedible prey (see Leibold et al. 1997). The assumed trade-off between resource exploitation and predator resistance among prey is central to the model's predictions.

Predator identity can modify the response of heterogeneous prey assemblages by affecting variation in edibility. For example, in plankton communities, large-bodied grazers such as *Daphnia* have higher filtering rates (e.g., Knoechel and Holtby 1986, Mourelatos and Lacroix 1990) and consume a broader size spectrum of algae (Burns 1968, Neill 1975a) compared to small-bodied cladocera (e.g., species of *Ceriodaphnia*, *Diaphanosoma*, etc.). Consequently, *Daphnia* are thought to more effectively control algal communities (Pace 1984, McQueen et al. 1986, Leibold 1989, Mazumder 1994). Within the context of the keystone predator model, inefficient predators with lower per capita feeding and prey conversion rates (i.e., conversion of prey consumed to growth) will result in higher prey biomass at equilibrium. Additionally, if predators can only consume a limited subset of the prey community inedible prey will result, further weakening top-down effects along gradients of productivity.

Despite the growing body of theory, remarkably few

experimental manipulations of both prey heterogeneity and productivity have been attempted, the exceptions being the microbial study of Bohannan and Lenski (1999) and the mesocosm study of Leibold and Wilbur (1992). In the following experiment, I employed an aquatic system in which the top predator was composed of a single species of zooplankton (either *Daphnia* or *Ceriodaphnia*), algae were prey, and basal resources were nutrients (phosphorus and nitrogen). Two model communities were established: a simple food chain composed of a single top predator and a single species of algae, and a more complex food web composed of a single top predator and a heterogeneous (i.e., diverse) algal community. Productivity was then manipulated by adding nutrients. If within-trophic-level heterogeneity is a key factor, communities with diverse algal prey should display positive correlations between trophic level biomass and productivity, whereas food chains should exhibit the classic EEH response (increases in zooplankton biomass and no change in algae). Additionally, food webs should harbor a greater relative abundance of less edible species of prey under conditions of nutrient enrichment. Because algal productivity is channeled into less edible forms in this situation, we expect zooplankton to respond positively to enrichment but this increase should be lower in magnitude when compared to food chains with completely edible prey (Bohannan and Lenski 1999). Finally, predator identity should further modify the degree of heterogeneity and hence the discrepancy between EEH and observed responses of food webs.

The aforementioned model predictions are based on the assumption that systems have reached a stable equilibrium. Experimentally, steady state conditions are difficult to obtain. An ideal experiment should last long enough to allow transient dynamics to diminish. Yet, in reality, the time frame required to obtain true steady state conditions is often sufficiently long to permit the intrusion of experimental artifacts (namely the invasion of new species or loss of nutrients from the system). The present experiment lasted six weeks, as a compromise between these issues, and was long enough to encompass several generations of predator and prey. Data analyses will rely largely upon exploration of dynamics to address model mechanisms. I discuss the validity and caveats of this approach in greater detail and in light of experimental results in the *Discussion*.

METHODS

The experiment was conducted indoors, under controlled environmental conditions, at the Kellogg Biological Station (KBS), Experimental Pond Facility (Hickory Corners, Michigan, USA). My experimental system consisted of white 20-L polyethylene containers artificially illuminated with 80-W overhead fluorescent fixtures equipped with full spectrum bulbs. Enclosures received continuous 24-h light. Room temperature was regulated and water temperature remained within 20 to

21°C. All enclosures received 18 L of well water (the same water used to culture all zooplankton). A $2 \times 2 \times 2$ fully factorial design was then employed. Treatments were: two levels of productivity (low vs. high) crossed with two levels of algal-prey heterogeneity (a single species "food chain" treatment vs. a diverse "food web" treatment) crossed with two zooplankton treatments (*Daphnia pulex* vs. *Ceriodaphnia quadrangula*). All treatments were replicated three times for a total of 24 enclosures.

Productivity was manipulated through addition of phosphorus (Na_2HPO_4) with high productivity treatments receiving a starting concentration of 180 $\mu\text{g P}$ per liter (well within the range considered hypereutrophic) and low productivity treatments receiving no additions for an initial concentration of 6 $\mu\text{g P/L}$. Nitrogen (NaNO_3) was added with phosphorus in a 36:1 N to P molar ratio. This naturally high ratio was matched to that of the untreated well water to avoid changes in algal stoichiometry, and helped ensure that the system was limited by a single nutrient, phosphorus (Hecky and Kilham 1988). It also made it unlikely that nutrient retention/recycling by zooplankton could have shifted the system from phosphorus to nitrogen limitation (Sterner et al. 1992, Sterner and Hessen 1994). Nutrients were added once at the start of the experiment.

Single species algal-prey treatments were established with a lab-cultured inoculum of *Monoraphidium* unknown sp., a unicellular species of green algae known to be both highly edible and nutritionally adequate for both species of zooplankton (C. Steiner, *personal observation*). To minimize addition of algal culture medium, algae were first settled for 24 h in a 1-L bottle. Excess medium was then decanted leaving an algal concentrate that was then diluted to 1 L in deionized water. Single prey treatments received a low-density inoculation of *Monoraphidium* resulting in a chlorophyll *a* start concentration of 0.25 $\mu\text{g/L}$. I established heterogeneous prey treatments by mixing *Monoraphidium* with an equal chlorophyll concentration of a diverse algal community extracted from ponds at the KBS pond facility. A 10-L sample of water was collected from the water column of each of three ponds using an integrated tube sampler and then filtered through 53- μm Nitex mesh to remove zooplankton. Samples were then pooled and thoroughly mixed before being added to enclosures. Total algal biomass after addition of both *Monoraphidium* and the diverse assemblage of algae equaled that of the single species enclosures (0.25 $\mu\text{g chlorophyll a/L}$). Approximately 800 mL of pond water was added to each enclosure. This low volume was unlikely to cause substantial changes in nutrient concentrations or N:P ratios. However, as a precaution, an equal volume of pond water was filtered through Gelman A/E glass fiber filters (removing all particles larger than 1 μm ; Gelman Sciences, Ann Arbor, Michigan, USA) and added to the single prey treatments.

Since most bacterioplankton are $<1 \mu\text{m}$ in size (Lampert and Sommer 1997), the addition of filtered pond water made it likely that all treatments (chains and webs) received a similar bacterial assemblage at the start of the experiment.

Examination of samples of the algal community added to the food web treatments revealed an assemblage diverse in taxa and morphologies. Of the forms known to achieve sizes outside the range of edibility, those present included pennate diatoms (Fragilariaceae, Naviculaceae), dinoflagellates (Peridinales, Gonyaulacales), *Dinobryon* communities (Dinobryaceae), and several species of filamentous algae. Also present, were a number of taxa in the edible ($<10 \mu\text{m}$) size range of zooplankton. These were primarily unicellular algae and flagellates (Chlorophyceae).

Zooplankton populations were established with low initial densities to avoid immediate overgrazing and population crashes at the start of the experiment, especially at low levels of productivity. *Daphnia* and *Ceriodaphnia* treatments each received nine haphazardly selected individuals concentrated from batch cultures. Cultures were established several months before the experiment by collecting *Daphnia pulex* and *Ceriodaphnia quadrangula* from several ponds in the area surrounding KBS. Species were isolated from samples and raised separately in untreated well water at high food density. Because *Daphnia* are larger than *Ceriodaphnia*, *Daphnia* treatments invariably received a larger biomass of zooplankton. However, given the low initial density relative to the potential population growth in these systems (see *Results*), the effects of differential biomass should have been minimal.

Algal growth on enclosure walls is largely inaccessible to zooplankton consumers and thus embodies a potential methodological artifact given the small size and high surface area to water volume ratio of the experimental enclosures. To minimize wall effects, I introduced snails (*Physa integra*) to both graze down algal growth and aid in recycling of nutrients to the planktonic community. Snails were obtained from ponds in the surrounding area, rinsed, and then lab reared in large culture vats for several months. Prior to the experiment, snails were lightly scrubbed and rinsed in well water. Each experimental enclosure then received five size-matched individuals at the start of the experiment.

Algae were added to enclosures immediately following addition of water, with zooplankton additions following two days later. A day after zooplankton inoculations, nutrients were added. All enclosures were gently mixed for 1 min every 4 h with low-pressure aeration from piston pumps. Mixing was intended to both resuspend algae and facilitate nutrient recycling within the water column. The experiment was allowed to run for 6 wk and enclosures were sampled weekly, beginning in the first week of the study for algae and the second week for zooplankton. Sampling was timed

to occur midway between mixing events. In each period, zooplankton were sampled by taking a 1.2-L sample of the water column using an integrated tube sampler. Zooplankton were then removed by filtering through 60- μm Nitex mesh and the water was returned to the source enclosure. Zooplankton were immediately preserved in acid Lugols solution and later enumerated in their entirety. Fifty randomly chosen individuals from each sample were measured to obtain biomass estimates from length–mass regressions. During each sample period, a 150-mL water sample was also extracted from each enclosure and filtered onto Gelman A/E glass fiber filters for subsequent analysis of chlorophyll *a* (sensu Welschmeyer 1994) as a correlate of algal biomass. Samples from single-prey treatments were filtered in their entirety to measure total chlorophyll *a*. Water samples from heterogeneous prey treatments were divided into two size fractions. Half of the sample was filtered directly to obtain estimates of total chlorophyll *a*. The other half was first filtered through 35- μm Nitex mesh to remove large algae, and then filtered onto glass fiber filters to measure the edible size fraction of algae. Size was chosen as a general indicator of edibility because it is a common constraint on dietary preference of zooplankton (Neill 1975a, Sommer 1988) and it is easily measured through size fractionation. Thirty-five microns was chosen as a proxy upper size limit for “highly edible” vs. “predator-resistant” prey. The maximum upper size limit of consumable prey for *Daphnia* is $\sim 60 \mu\text{m}$ (Burns 1968). *Ceriodaphnia* on the other hand have preferences that are much lower, below 10 μm (Neill 1975a). Thus, 35 μm represents a midpoint cutoff applicable to both predators (though in general, edibility may be overestimated for *Ceriodaphnia* and underestimated for *Daphnia*). It should be noted that nutrients were added only at the start of the experiment. Hence, all nutrient resupply occurred via natural recycling within the enclosures. Other than minimal losses from zooplankton and algal sampling (an imposed mortality rate of $\sim 7.5\%$ per wk), the enclosures represented closed systems.

Biomass responses of zooplankton and algae were analyzed using univariate repeated-measures ANOVA (rm-ANOVA). Initial (day 0) densities were not included in analyses. When necessary, analyses of biomass from single sample dates were performed using ANOVA. Relative biomass values were arcsine-square-root transformed. All other data were \log_{10} transformed to conform to assumptions of homogeneity of variances. Because samples taken on adjacent dates from a given experimental unit are likely to show greater covariance than nonadjacent samples, assumptions of repeated-measures ANOVA (sphericity) may be violated. To avoid type I errors when examining within subjects effects (i.e., response curves through time), both Greenhouse-Geiser (G-G) and Huynh-Feldt (H-F) ad-

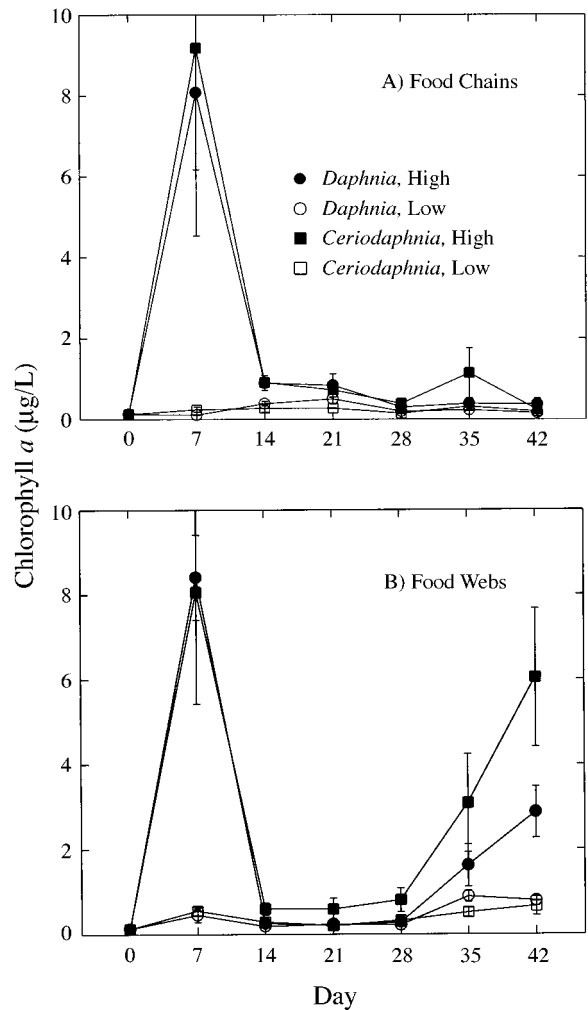


FIG. 1. Algal prey response over the course of the experiment in the presence of each predator and at low or high productivity for (A) food chains (single algal prey) and (B) food webs (heterogeneous algal prey). Values shown are means ± 1 SE.

justed probabilities are presented. All analyses were performed using Systat 8.0 (SPSS 1998).

RESULTS

Focusing first on prey responses, algae in both food chains and food webs displayed a large initial increase in biomass in response to the initial nutrient pulse and delayed responses of the predators (Fig. 1A, B). Biomass by day 14 had decreased as zooplankton populations responded numerically but nutrient enriched food webs demonstrated a second marked increase in algal biomass nearing the end of the experiment (Fig. 1B). There was a significant interaction of time, nutrients and heterogeneity (within subjects effect, G-G $P < 0.01$, H-F $P < 0.001$, $F_{4,64} = 6.79$). However, a significant between subjects interaction between nutrients and heterogeneity was not detected ($P = 0.193$,

TABLE 1. Univariate repeated-measures ANOVA testing for effects of predator identity, prey heterogeneity, nutrient enrichment, and time (i.e., sample date) on total chlorophyll *a*, for days 14–42.

A) Univariate between-subjects effects					
Source of variation	df	MS	F	P	
Predator identity	1	0.042	3.63	0.075	
Prey heterogeneity	1	0.240	20.82	<0.001	
Nutrients	1	0.575	49.85	<0.0001	
Predator × Prey heterogeneity	1	0.031	2.72	0.119	
Predator × Nutrients	1	0.084	7.31	0.016	
Prey heterogeneity × Nutrients	1	0.057	4.93	0.041	
Predator × Prey heterogeneity × Nutrients	1	0.031	2.71	0.119	
Error	16	0.012			
B) Univariate within-subjects effects					
Source of variation	df	MS	F	P (G-G)†	P (H-F)‡
Time (<i>T</i>)	4	0.122	22.00	<0.0001	<0.0001
<i>T</i> × Predator identity	4	0.003	0.62	0.584	0.649
<i>T</i> × Prey heterogeneity	4	0.227	40.97	<0.0001	<0.0001
<i>T</i> × Nutrients	4	0.039	7.07	<0.001	<0.0001
<i>T</i> × Predator × Prey heterogeneity	4	0.007	1.20	0.317	0.317
<i>T</i> × Predator × Nutrients	4	0.005	0.87	0.451	0.486
<i>T</i> × Prey heterogeneity × Nutrients	4	0.066	11.85	<0.0001	<0.0001
<i>T</i> × Predator × Prey heterogeneity × Nutrients	4	0.006	1.06	0.370	0.384
Error	64	0.006			

† Greenhouse-Geiser adjusted probability.

‡ Huynh-Feldt adjusted probability.

$F_{1,16} = 1.84$). The lack of significance was likely a result of the large spike in algal biomass on day 7, present in both webs and chains. This early date represents prey responses under little or no predation pressure and is thus not representative of dynamics expected in the keystone model. When excluding day 7 and analyzing responses from days 14 (after predators had time to respond) to 42, a significant between-subjects interaction between nutrients and prey heterogeneity was detected (Table 1). Note that increases in algal biomass in food webs at the end of the experiment approached the maximal (day 7) levels, indicating that productivity treatments were still robust.

The degree of divergence in biomass in food webs relative to food chains was best seen when examining algal biomass on the final date of the experiment. Responses to productivity were subdued in single-species enclosures, in clear contrast to the large increases in biomass of heterogeneous prey with enrichment (Fig. 2A, B; a result borne out by a significant nutrient by heterogeneity interaction; $P < 0.00001$, $F_{1,16} = 27.82$; Table 2). In those communities with only a single species of algae, there were no significant effects of nutrient enrichment on biomass, regardless of predator identity (Fig. 2A, B; $P > 0.87$, Tukey's *hsd*). In contrast, algal biomass in nutrient enriched food webs was significantly greater than all other treatments, independent of predator identity (Fig. 2A, B; $P < 0.05$ for all comparisons, Tukey's *hsd*).

While edible algae (<35 μm) comprised the majority of algal biomass during the early spike in prey biomass (day 7), this size fraction was greatly reduced as predators increased in abundance (Fig. 3A, B). Focusing

on days 14–42, there were no significant effects of nutrient enrichment on the edible size fraction using repeated measures ($P > 0.29$, for all between- and within-subjects effects and interactions), nor was there a nutrient effect when examining just day 42 abundances ($P > 0.60$, two-way ANOVA). In contrast, nutrient enrichment had a positive effect on resistant algae over time ($P < 0.0001$, $F_{1,8} = 54.96$, between subjects effect, rm-ANOVA) and on day 42 ($P < 0.001$, $F_{1,8} = 45.97$, two-way ANOVA). Thus, the increases in total chlorophyll *a* on days 28–42 (Fig. 1B) were due purely to responses of resistant algae (Fig. 3A, B). These results were mirrored in analyses of relative biomass of resistant prey, calculated as the difference between total and <35 μm chlorophyll *a* divided by total chlorophyll *a*. Relative abundance of large algae was greatly enhanced by enrichment, showing a nearly fourfold increase by experiment's end (Fig. 4; between subjects effect of nutrients, $P < 0.001$, $F_{1,8} = 31.61$, two-way rm-ANOVA). Though the species composition of the resistant algal fraction was not quantified, examination of net phytoplankton (species >60 μm) revealed an assemblage dominated by filamentous green algae followed by the large dinoflagellate *Ceratium*. Colonial forms of *Monoraphidium* were not observed, which would have complicated interpretations considerably.

There was evidence of an effect of predator identity on total algal biomass, but the effect was only manifest in high-productivity treatments (Fig. 1A, B). There was a trend for a nutrient by predator interaction when examining all six sample dates (between subjects effect, $P = 0.061$, $F_{1,16} = 4.06$). The interaction was clearer when analysis was restricted to days 14–42 (between-

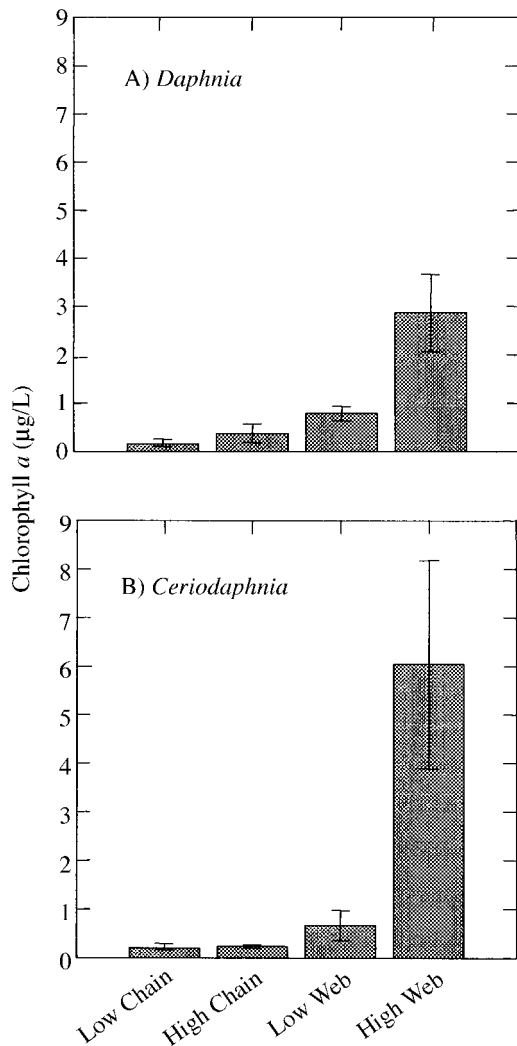


FIG. 2. Algal biomass on the final day of the experiment in the presence of (A) *Daphnia* predators or (B) *Ceriodaphnia* predators. Treatments shown are algal heterogeneity (chains vs. webs) and productivity (low vs. high). Values shown are means \pm 1 SE.

subjects effect, $P = 0.016$, $F_{1,16} = 7.31$). I performed separate analyses for low and high nutrient treatments for days 14–42, testing for effects of predator identity and prey heterogeneity. A between-subjects predator

effect was not detected in low-productivity treatments regardless of prey composition ($P = 0.209$, $F_{1,8} = 1.87$). In high-productivity treatments, however, algal biomass was lower in the presence of *Daphnia* compared to *Ceriodaphnia*, (between-subjects effect, $P = 0.043$, $F_{1,8} = 5.81$). When examining total algal biomass on the final date of the experiment, there was some indication of a three-way interaction between predator identity, prey heterogeneity and enrichment, but the effect was not significant at the 0.05 level (Table 2). While predators did not differ in their effects on the edible size fraction ($P > 0.10$, rm-ANOVA), a significant predator by nutrient interaction was detected when examining responses of predator-resistant algae (between-subjects effect, $P = 0.048$, $F_{1,8} = 5.45$). *Daphnia* more strongly limited resistant algae but only at high productivity levels (Fig. 3A, B). Predator identity had weak effects on the relative abundance of edible vs. resistant algal prey ($P = 0.067$, two-way rm-ANOVA).

Zooplankton biomass responses depended on predator identity, nutrient enrichment, and algal heterogeneity. Both species responded positively to enrichment, regardless of the prey community presented, but *Daphnia* showed larger responses under conditions of enhanced productivity over time (Fig. 5). A significant interaction between nutrient enrichment and predator identity was detected when using rm-ANOVA (Table 3). Differential responses of the two predators to the composition of the prey community and productivity were best perceived when inspecting each separately. As predicted by theory, both zooplankters exhibited trends towards lower biomass responses to enrichment in food webs compared to food chains (Fig. 5A, B) but a significant interaction between enrichment and prey heterogeneity was not detected for either (between- and within-subjects effects, $P > 0.15$, two-way rm-ANOVA for each predator separately). Only positive main effects of enrichment were detected for both *Ceriodaphnia* ($P < 0.01$, $F_{1,8} = 21.07$) and *Daphnia* ($P < 0.0001$, $F_{1,8} = 89.30$) using repeated-measures ANOVA.

DISCUSSION

The top-down, bottom-up debate has routinely espoused two very different and opposing points of view:

TABLE 2. Results of three-way analysis of variance testing for effects of predator identity, prey heterogeneity, and nutrient enrichment on total chlorophyll *a* on the final sample date.

Source of variation	df	MS	F	P
Predator identity	1	0.012	1.24	0.283
Prey heterogeneity	1	0.830	86.36	<0.0001
Nutrients	1	0.387	40.21	<0.0001
Predator \times Prey heterogeneity	1	0.020	2.12	0.165
Predator \times Nutrients	1	0.018	1.92	0.185
Prey heterogeneity \times Nutrients	1	0.268	27.82	<0.0001
Predator \times Prey heterogeneity \times Nutrients	1	0.043	4.43	0.051
Error	16	0.010		

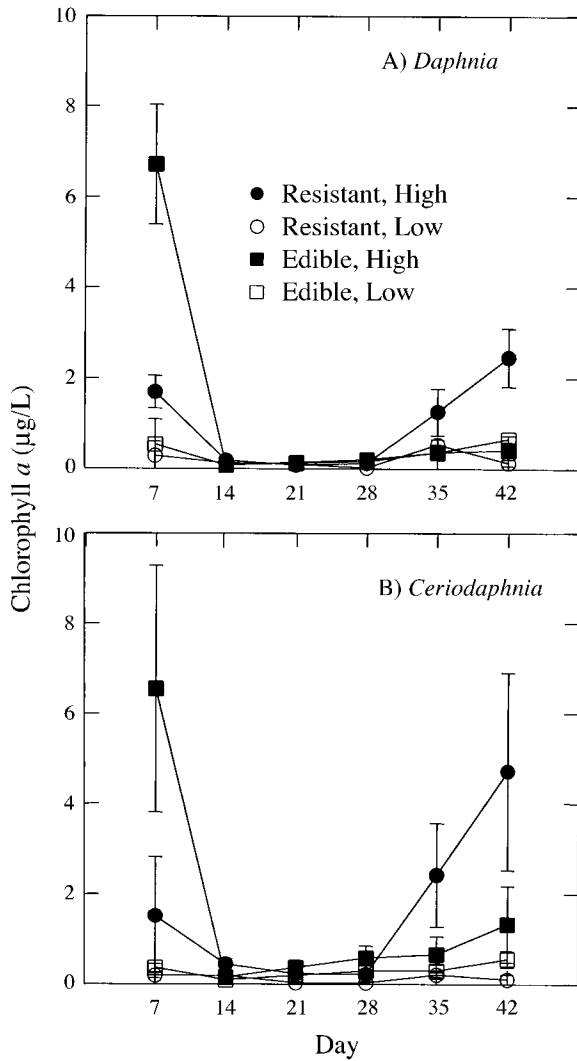


FIG. 3. Responses of "edible" (<35 µm) and "resistant" (>35 µm) size fractions of algae over time at low or high productivity for (A) *Daphnia* treatments and (B) *Ceriodaphnia* treatments. Initial (day 0) algal samples were not size fractionated. Values shown are means ± 1 SE.

either systems exhibit donor-control dynamics in which trophic cascades are rare and resource limitation dictates trophic-level biomass (e.g., White 1978, Strong 1992, Polis and Strong 1996) or systems harbor the potential for strong consumer–resource interactions in which top-down control alternates with bottom-up control at different trophic levels (e.g., Hairston et al. 1960, Oksanen et al. 1981, Oksanen and Oksanen 2000). However, recent treatments have emphasized a pluralistic approach in which both consumer and resource effects jointly determine trophic-level biomass (e.g., Leibold 1996, Osenberg and Mittelbach 1996, Leibold et al. 1997). In the keystone predator model, for example, top-down effects are dampened but both predators and resources determine total prey abundance. Moreover, the model accounts for shifts in community

composition and diversity while explicitly considering underlying mechanisms, a significant departure from earlier treatments (e.g., Arditi and Ginzburg 1989). Thus, validation of the keystone model and the effects of prey heterogeneity are of potential import for understanding the myriad of community dynamics and patterns we see in natural systems.

The results of this experiment demonstrate that within-trophic-level heterogeneity can have substantial effects on predator–prey dynamics and community structure. Simple food chains exhibited patterns of trophic biomass partitioning in keeping with predictions of EEH. Prey biomass showed little or no relationship with productivity, while predator biomass was positively affected, suggesting that predators exerted strong top-down effects. In contrast, when communities were composed of food webs, both predators and prey responded positively to enrichment. The increases in algal biomass in food webs were due entirely to increases in the large size fraction of algae, a pattern consistent with species turnover in the prey community and a shift in dominance towards predator-resistant prey (i.e., a keystone effect). Finally, because shifts in prey composition can allow system productivity to be channeled to species inaccessible to predators, theory predicts that predator responses to enrichment should be lower in food webs compared to food chains. In general, results from both predator treatments supported this prediction but trends were not significant at the $P = 0.05$ level.

These results are consistent with a hypothesized trade-off between competitive ability and predator resistance among algal species in food webs. While I did not directly address the trade-off issue (a predator ex-

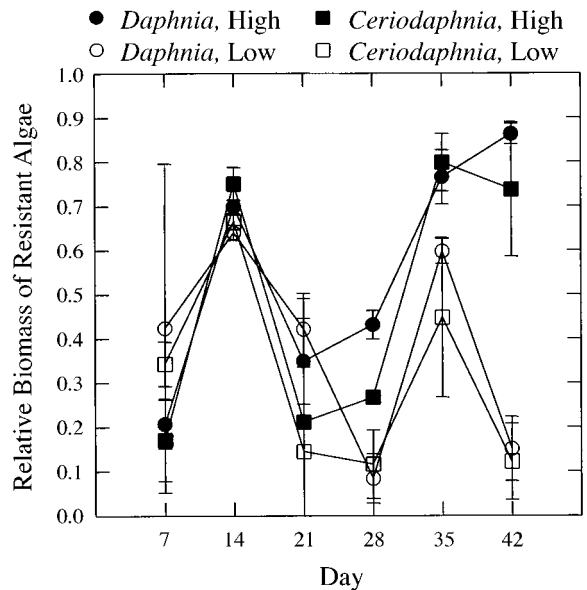


FIG. 4. Dynamics of relative biomass of predator-resistant algae (in food webs) over the course of the experiment. Shown are mean responses to predator identity and productivity ± 1 SE.

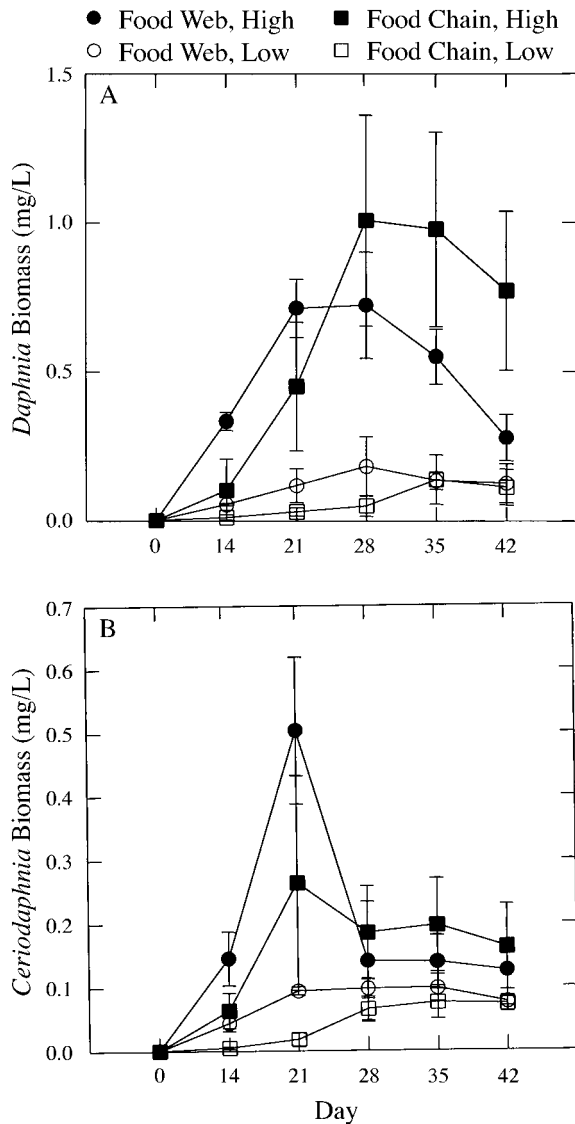


FIG. 5. Predator biomass response over the course of the experiment in food webs or food chains, and at low or high productivity levels, for (A) *Daphnia* and (B) *Ceriodaphnia*. Note differences in scale. Values shown are means \pm 1 SE.

clusion treatment was not included), a number of other studies have shown that smaller algal size generally leads to higher rates of nutrient uptake and population increase, suggesting that these species are superior resource competitors (reviewed in Reynolds 1984). Given that size is known to lead to decreased rates of zooplankton consumption, the existence of the trade-off appears to be a relatively sound assumption but one that clearly requires future experimental validation.

This study also examined the effect of consumer identity as a potential determinant of trophic structure. It is a widely held truism that large-bodied *Daphnia* are strong interactors with algae and thus more effectively limit their prey communities compared to small-

bodied species of zooplankton (Leibold 1989). Yet, a number of studies call into question the generality of this assertion (e.g., Leibold and Wilbur 1992, Turner and Mittelbach 1992, Leibold et al. 1997). My results suggest that ecological context plays an important role in mediating the effects of consumer size on the strength of zooplankton–algae interactions. *Daphnia* and *Ceriodaphnia* were comparable in their ability to control algal biomass at low productivity. However, *Daphnia* were able to effect larger reductions in algal prey under enriched conditions (Fig. 1A, B). The two consumers also diverged in their effects on algae in food webs. While both affected edible algae to a similar degree, *Daphnia* more effectively controlled biomass of resistant algae in high-nutrient treatments. This is not unexpected given *Daphnia*'s known ability to feed on large algal particles, well outside the range of small-bodied species; the same algae favored under high-nutrient conditions. Thus, my results support the argument that effective control of algal communities along gradients of enrichment is dependent not on prey heterogeneity alone but on the identity of their zooplankton consumers.

As with any experimental system, especially one that strives to address theory, a number of important caveats and concerns must be addressed. First, because my study system was not conducted under sterile conditions, food chain treatments were prone to invasion by predator-resistant algae. The relatively short duration of this experiment was intended to minimize this problem. To monitor invasives, I size fractionated water samples from food chains at days 21 and 42 of the experiment. By midexperiment, large algae had begun to appear in some food chain enclosures (in low-nutrient treatments, mean relative biomass of $>35 \mu\text{m}$ algae = 0.073, range = 0.000–0.206; in high-nutrient treatments, mean = 0.101, range = 0.050–0.146) and had reached greater proportions by the termination of the experiment (in low-nutrient treatments, mean relative biomass = 0.169, range = 0.000–0.392; in high-nutrient treatments, mean = 0.393, range = 0.000–0.607). Thus, a longer experimental duration would likely have resulted in algal dynamics in food chain treatments similar to those of the food webs. Note, however, that invasions actually make detection of nutrient effects in food chains more likely (assuming they respond in the same manner as the food web treatments) and differences between chains and webs more difficult to detect. To explore the degree to which invading resistant algae affected my results, I reanalyzed data after eliminating replicates of food chain treatments with $>25\%$ invasion by predator-resistant algae at the end of the experiment. Using *t* tests to perform pairwise comparisons on algal biomass for the final date, when effects of invasives should have been most severe, results were similar to those using the full data set. There were no significant differences detected between low and high nutrient treatments in the food chains, though

TABLE 3. Univariate repeated-measures ANOVA testing for effects of predator identity, prey heterogeneity, nutrient enrichment, and time (i.e., sample date) on predator biomass over the course of the experiment (days 14–42).

A) Univariate between-subjects effects					
Source of variation	df	MS	F	P	
Predator identity	1	0.126	46.44	<0.0001	
Prey heterogeneity	1	0.001	0.29	0.595	
Nutrients	1	0.296	109.03	<0.0001	
Predator × Prey heterogeneity	1	0.002	0.68	0.422	
Predator × Nutrients	1	0.084	30.77	<0.0001	
Prey heterogeneity × Nutrients	1	0.005	1.82	0.197	
Predator × Prey heterogeneity × Nutrients	1	0.004	1.48	0.241	
Error	16	0.003			
B) Univariate within-subjects effects					
Source of variation	df	MS	F	P (G-G)†	P (H-F)‡
Time (T)	4	0.017	12.64	<0.0001	<0.0001
T × Predator identity	4	0.008	5.99	0.004	0.0005
T × Prey heterogeneity	4	0.010	7.01	0.002	<0.001
T × Nutrients	4	0.008	5.61	0.006	<0.001
T × Predator × Prey heterogeneity	4	0.002	1.35	0.274	0.263
T × Predator × Nutrients	4	0.006	4.58	0.014	0.003
T × Prey heterogeneity × Nutrients	4	0.006	4.28	0.018	0.005
T × Predator × Prey heterogeneity × Nutrients	4	0.002	1.31	0.283	0.276
Error	64	0.001			

† Greenhouse-Geiser adjusted probability.

‡ Huynh-Feldt adjusted probability.

power is admittedly low ($P = 0.284$ for *Daphnia* treatments, $P = 0.940$ for *Ceriodaphnia*).

A second point to consider is that the Leibold (1996) keystone predation model and EEH food chain model both base predictions on the assumption that all community components have attained a stable equilibrium. Hence, a valid concern is whether the present experiment allows us to address these models. Qualitatively, algal biomass in food chains as well as edible algae in food webs appeared relatively stable, but it was clear that resistant algae in food webs had not stabilized. Furthermore, *Daphnia* showed a pronounced drop in abundance in nutrient enriched food webs in the final two weeks of the experiment (Fig. 5A). This may have been due to the shift in dominance to large inedible algae combined with the genus' known propensity for starvation in juvenile stages (Neill 1975b, Romanovsky and Feniova 1985). Of concern is whether algal dynamics, specifically the increase in biomass of heterogeneous prey in *Daphnia* treatments, were a result of the aforementioned keystone processes or the drop in predator abundance. Two lines of reasoning support my conclusions. First, heterogeneous prey in the presence of *Daphnia* showed responses to productivity that paralleled those of *Ceriodaphnia* (Fig. 2B), suggesting that increases were not simply a result of decreases in predator abundance. That heterogeneous prey composition shifted towards larger, presumably less edible, forms with enrichment further supports the assertion that keystone processes were operating.

Finally, inferring future dynamics from the present prey trajectories is potentially hampered if predators were to exhibit cyclic oscillations (e.g., stable limit

cycles). This is especially true if unstable predator dynamics somehow deter dominance by inedible algae. *Ceriodaphnia* biomass appeared stable but *Daphnia* species are known to display an array of population behaviors from sustained, stable population levels over time to cyclic oscillations (Murdoch and McCauley 1985). Using simulations, Bohannan and Lenski (1999) show that keystone processes can be robust to such instabilities; oscillations in predator and edible prey abundances do not deter invasion and dominance by inedible prey under enriched conditions. This prediction was confirmed in their experimental results. Abrams (1999) presents a general theoretical treatment of the ability of predator-resistant prey to invade an unstable system composed of a top predator and competitively superior edible prey. His results show that invasion can be hindered by predators that exhibit limit cycles, though invasibility is less restricted for those prey that are close to or completely inedible. Given these studies, consequences of cyclic *Daphnia* dynamics on prey responses in my experiment are uncertain. Accordingly, results from *Daphnia* treatments should be viewed with some caution. Ultimately, this question can only be resolved empirically and, given Abrams (1999) analyses, is a potentially important avenue of research to pursue. Yet, this would require an experimental duration much greater than the one I utilized, on the order of several months. Given the aforementioned caveats, I have attempted to enhance the robustness of my conclusions by combining analyses of dynamics (using repeated-measures ANOVA) with examination of biomass at the end of the experiment. Even if we rely solely on *Ceriodaphnia* treatments, this

combined analysis clearly indicates that prey heterogeneity can have important effects on patterns of biomass partitioning and the relative importance of top-down vs. bottom-up processes. Algal biomass and size structure exhibited trajectories and divergences that were consistent with model predictions and hypothesized mechanisms.

In addition to prey heterogeneity, a number of alternative hypotheses have been proposed as potential explanations for why natural patterns of trophic-level biomass commonly deviate from EEH predictions. While some of the proposed mechanisms may have operated in my experiment, none appear to fully explain my results. These hypotheses include: (1) stage-structured interactions in which resources of juvenile and adult stages of predators are decoupled (Mittelbach et al. 1988, Persson et al. 1988, 1992), (2) adaptive responses by foraging prey (Abrams 1996), (3) unstable predator-prey dynamics (Abrams and Roth 1994), (4) spatial heterogeneity in the top predator (Arditi and Saiah 1992, Abrams 1994), (5) interference among predators (Sarnelle 1994, McCarthy et al. 1995, Oksanen et al. 1995), (6) increases in zooplankton death rates with productivity as a result of increasing planktivory (McCauley et al. 1988, Sarnelle 1992), and (7) ratio dependence in predator functional responses (Arditi and Ginzburg 1988, Akcakaya et al. 1995). Hypotheses 1, 2, and 6 may be immediately dismissed as inapplicable to the present experiment. There was no evidence of predator-prey oscillations allowing rejection of hypothesis 3. Finally, hypotheses 4, 5, and 7 could have all occurred to some degree in my experiment. However, there is no obvious reason why these processes should have operated differentially in food chain and food web enclosures. Hence, they cannot explain observed differences between chains and webs.

This experiment represents one of only a handful in which the effects of prey heterogeneity were explored experimentally. Although a number of studies have experimentally documented keystone effects of predators on the composition of prey communities (e.g., Paine 1966, Levin et al. 1977, Lubchenco 1978, McCauley and Briand 1979), few have actually manipulated the prey assemblage or compared food chains to food webs with the intent of exploring trophic-level limitation. A notable exception is the microbial study of Bohannan and Lenski (1999). Their examination of food-chain and food-web responses to enrichment supported theoretical predictions and produced results similar to mine. Leibold and Wilbur (1992) also uncovered effects of within-trophic-level heterogeneity on patterns of trophic-biomass response to productivity in their aquatic mesocosms. However, in their study, food web architecture alone was manipulated; food chains were not compared with food webs. The importance of these experimental results is bolstered by several lines of indirect evidence implicating prey heterogeneity as an important factor governing the organization of natural

aquatic communities. Recent survey data and reviews of the literature indicate that the mechanisms of the keystone-predator model may be operating among water bodies to generate patterns of trophic structure and community composition (Leibold et al. 1997, Leibold 1999). Furthermore, increases in grazer-resistant forms of phytoplankton are commonly observed in water bodies along gradients of nutrient enrichment (Reynolds 1984, McCauley et al. 1988, Paerl 1988, Watson et al. 1992), and the presence of zooplankton has been shown experimentally to favor the incidence of inedible forms of algae, in keeping with model expectations (McCauley and Briand 1979, Vanni 1987). There are a plethora of ecological mechanisms that can weaken predator effects and result in correlated biomass among adjacent trophic levels (e.g., Power 1992, Abrams and Roth 1994, Persson et al. 1996, Polis and Strong 1996), and certainly this study does not discount the alternatives. However, my results combined with previous investigations clearly show that along gradients of productivity, the presence of a diverse prey assemblage can have profound effects on predator-prey dynamics, trophic structure and the strength of predator control.

Though community ecology has long operated under the aegis of the mechanistic approach, tests of theory such as the keystone-predator model are regrettably few. The focus on mechanism advances our understanding beyond the insights provided by phenomenological treatments by explicitly incorporating the biology underlying community dynamics and species interactions. This knowledge gained then offers the prospect of a greater capacity for predicting natural ecological patterns. While my study addresses the effects of food web structure it does not explicitly test for the underlying autecological traits and trade-offs assumed to operate in the model. These traits will in general have physiological, morphological, or behavioral bases to them and can be subject to selection. Thus, further examination of such mechanisms could offer an exciting linkage between evolutionary ecology and the ecological study of traits governing species coexistence.

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