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Keystone predator effects and grazer control of planktonic primary production

Christopher F. Steiner

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If prey species exhibit trade-offs in their ability to utilize resources versus their ability to avoid predation, predators can facilitate prey turnover along gradients of productivity, shifting dominance from edible to inedible prey (the keystone predator effect). I tested this model under controlled, laboratory conditions, using a model aquatic system composed of zooplankton as the top consumer, a diverse community of algae as prey, and nutrients as basal resources. Nutrient manipulations (low and high) were crossed with presence–absence of zooplankton. Results supported theoretical predictions. Algal biomass increased in response to enrichment regardless of predator presence/absence. However, predators and nutrients had an interactive effect on algal biomass and size structure. At the low nutrient level, algal-prey were dominated by edible forms and attained similar biomass regardless of zooplankton presence/absence. At the high level of enrichment, presence of zooplankton favored higher levels of algal biomass and shifted dominance to large, inedible taxa. At the termination of the experiment, I performed a series of lab-based assays on the resultant algal community in order to quantify trade-offs among algal size classes in maximal population growth rates (as a measure of competitive ability for nutrients) and susceptibility to zooplankton grazing. Assays provided support for a size-based keystone trade-off. Small size classes of algae displayed higher maximal growth rates but were more susceptible to grazing effects. Large size classes were protected from grazing but showed low rates of population growth in response to enrichment.

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Keystone predator effects occur when predators suppress prey that are superior resource competitors, permitting less competitive, predator-resistant prey to persist within a community. This form of top-down regulation received its first cogent expositions in the pioneering studies of Brooks and Dodson (1965) and Paine (1966) and has since resurfaced repeatedly in varied forms and guises (Levin et al. 1977, Lubchenco 1978, Vance 1978, McCauley and Briand 1979, Leibold 1989, 1996, Holt et al. 1994, Bohannan and Lenski 1999, 2000, Chase et al. 2000). Most recently, the keystone model has been recast to explain how the biomass of trophic levels within communities may change with increasing productivity (Leibold 1996, Leibold et al. 1997, Chase et al. 2000), a basic pattern whose underlying drivers remain a fundamental topic in community ecology.

Debate over the relative importance of consumer versus resource effects has frequently centered on patterns of biomass partitioning (Hairston et al. 1960, Power 1992, Leibold et al. 1997, Oksanen and Oksanen 2000). A catalyst of dispute has been the mismatch between patterns observed in nature and those predicted from early food chain theory (Oksanen et al. 1981). These models predict that the equilibrial biomasses of adjacent trophic levels are not correlated along gradients of productivity. Instead, only top predators and every other trophic level below them are

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predicted to increase as potential productivity increases (Mittelbach et al. 1988). Therefore, the biomass of a predator trophic level is not correlated with the biomass of its prey. Such patterns appear to be quite rare in nature. A cursory survey of existing data suggests that the abundance of trophic levels in natural systems commonly increase in unison with increasing productivity (McCauley and Kalff 1981, Hanson and Peters 1984, McNaughton et al. 1989, Ginzburg and Akcakaya 1992, Cyr and Pace 1993, Leibold et al. 1997).

The divide between model prediction and observation can be remedied by explicitly incorporating heterogeneity of species within trophic levels (Abrams 1993, Holt et al. 1994, Leibold 1996). For example, if prey species within a trophic level share the same top predator and exhibit trade-offs in their competitive ability versus their susceptibility to predation, a serial replacement of prey can occur as prey resources increase (i.e. as potential productivity increases; Leibold 1996). Prey that are strong resource competitors are expected to dominate at low levels of potential productivity; augmenting prey resources permits less efficient competitors but more predator-resistant prey to invade and dominate. This is the familiar keystone predator effect and the underlying trade-off among prey can be termed the "keystone trade-off." A consequence of this phenomenon is that both predator and prey biomass are expected to increase jointly with increasing production (Leibold 1996, Leibold et al. 1997). Hence, this model of combined top-down and bottom-up limitation may, in part, account for observed natural patterns of biomass partitioning.

In freshwater planktonic communities, zooplankton and phytoplankton biomasses are commonly correlated with each other and with measures of planktonic productivity (McCauley and Kalff 1981, McCauley et al. 1988, Leibold et al. 1997). There is evidence that the keystone trade-off may operate among planktonic algae (Leibold et al. 1997, Agrawal 1998); similar claims have been made for benthic algae in streams and in marine systems as well (Rosemond et al. 1993, Sommer 1997, Hillebrand et al. 2000). For example, small algal size generally leads to higher susceptibility to zooplankton grazing (reviewed by Sterner 1989). Yet, smaller algal taxa tend to have higher rates of population increase compared to large taxa, suggesting that they may be better competitors for shared nutrient resources (reviewed by Reynolds 1984, 1989). Moreover, both observational and experimental studies have shown that nutrient enrichment facilitates increases in grazer-resistant forms of phytoplankton (Reynolds 1984, McCauley et al. 1988, Paerl 1988, Watson et al. 1992, Steiner 2001), and zooplankton presence often favors the incidence of inedible algal taxa (McCauley and Briand 1979, Vanni 1987, Kerfoot et al. 1988). While these lines of evidence are in accordance with model assumptions and expectations, stronger supporting evidence would be afforded by an experiment that crosses presence and absence of zooplankton-grazers with manipulations of nutrient enrichment. This design permits detection of the interactive effects of grazing and nutrient concentration. To date, aquatic studies that have simultaneously manipulated grazer presence/absence and nutrients have used experimental durations on the order of a few days to a week (Lehman and Sandgren 1985, Elser and Goldman 1991, Gonzalez 2000), time periods much too short to approach steady state conditions (a requisite to properly address model predictions). Though there are numerous longer-term studies that have crossed manipulations of nutrients with planktivorous fish presence/absence (reviewed by Brett and Goldman 1996, and Leibold et al. 1997), these experiments are far from ideal for addressing keystone effects on algae. While fish can strongly depress zooplankton populations, they often do not completely remove grazers; instead large zooplankton taxa are selectively removed, shifting dominance to small-bodied species (Brooks and Dodson 1965, Gliwicz and Pijanowska 1989). Moreover, fish themselves can have important indirect effects on algae via nutrient recycling (Vanni and Layne 1997).

In this paper, I present results of an experiment in which I tested the keystone model under controlled, laboratory conditions. I utilized a model aquatic system composed of a single species of zooplankton as the top consumer, a diverse community of algae as prey, and nutrients as basal resources. Treatments consisted of manipulations of productivity (in the form of two levels of nutrient enrichment) crossed with presence-absence of zooplankton. The experiment was allowed to run for ten weeks, long enough to encompass several generations of zooplankton and algal-prey. At the termination of the experiment, I performed a series of lab-based assays on the resultant algal community in order to quantify trade-offs among algal size classes in maximal population growth rates (as a measure of competitive ability for nutrients) and susceptibility to zooplankton grazing. If keystone effects are occurring (sensu Leibold 1989, 1996), algal biomass should increase in response to enrichment in the presence and absence of zooplankton, though this increase should be greater in the latter. Furthermore, edible algae are predicted to dominate in the absence of zooplankton regardless of nutrient level. In the presence of zooplankton, algal composition is predicted to shift to dominance by inedible forms at high levels of enrichment. Finally, if a size-based keystone trade-off exists among algae, I predict that in assays large size classes of algae will display lower population growth rates but be less susceptible to grazing.

Methods

The experiment was performed indoors at the Kellogg Biological Station (Hickory Corners, Michigan, USA). Air temperature remained between 20.5–22°C. Experimental enclosures consisted of 18 l, polyethylene containers with mesh screening affixed on tops to deter insect invasion. Enclosures received 24 h illumination with fluorescent light fixtures, each equipped with two full-spectrum, 40 W bulbs. The experimental design consisted of a 2×2 factorial manipulation – zooplankton presence and absence (hereafter, $+Z$ and $-Z$) crossed with two levels of nutrient enrichment (nutrient addition versus no addition; hereafter, $+N$ and $-N$). All treatments were replicated four times. I utilized a random complete block design, where each light fixture acted as a block.

Enclosures were filled with 15.2 l of untreated well water and then inoculated with a natural algal assemblage obtained from ponds at the K.B.S. experimental pond facility. Nine liter water samples were collected from four ponds using a 1.3 m long, integrated tube sampler then filtered through a 53 μm mesh to remove zooplankton. Samples were then pooled, mixed, and 1 l added to each enclosure, raising the final volume to 16.2 l. Examination of subsamples of algal inocula revealed a taxonomically and morphologically diverse algal assemblage composed of diatoms, desmids, colonial and filamentous green algae, chrysophytes, colonial and filamentous cyanobacteria, and small edible species of green algae.

I chose *Ceriodaphnia quadrangula* (a small-bodied cladoceran and generalist filter feeder) as my focal zooplankter (hereafter referred to by genus). Two months prior to the experiment, *Ceriodaphnia* individuals were collected from a pond in the area, isolated, and raised in batch cultures under high food conditions. Two days following phytoplankton additions, zooplankton were collected from cultures, rinsed on a 250 μm mesh, and resuspended in well water. Sixteen randomly chosen individuals were then added to each $+Z$ treatment. Because algae and bacteria from zooplankton cultures may have accompanied *Ceriodaphnia* during additions, I created an inoculum of zooplankton culture water by collecting 2 l of water from cultures and filtering through 80 μm mesh to remove zooplankton. I then added 100 ml to all experimental containers.

Nutrients were added on the same day as zooplankton (henceforth referred to as day 0). Manipulations consisted of additions of phosphorous (as KH_2PO_4) resulting in an initial concentration of 100 $\mu g\, l^{-1}$. $-N$ treatments received no nutrient additions for a starting concentration of 18 $\mu g\, l^{-1}$. Nitrogen (as NH_4NO_3) was also added to $+N$ enclosures in a 17:1 N:P molar ratio matched to that of the untreated well water. Nutrients were added once at the start of the experiment.

To further ensure that all enclosures received the same initial phytoplankton assemblage, I redistributed algae among all enclosures four days following nutrient additions. Enclosures were gently mixed and 300 ml of water was sampled from each. Zooplankton were removed by filtering through 250 μm mesh and returned to respective enclosures. To further ensure zooplankton removal, all water samples were then pooled and CO_2 added in the form of carbonated water (20% of volume). Zooplankton were allowed to settle for 15 minutes and zooplankton-free water was then decanted, aerated and equally redistributed among all enclosures.

Zooplankton and algae were sampled weekly beginning on day 8 up to day 43, after which enclosures were sampled every two weeks up to day 71, the final sample date. During each sample period, I collected phytoplankton by removing 400 ml of water from each enclosure using a tube sampler that integrated the water column. Care was taken to not disturb bottom sediments. Samples were stored on ice, in the dark, and later divided into two 150 ml sub-samples. Though several traits may affect resistance to grazing, I focused on algal size as a key determinant of edibility since it is known to be an important constraint on dietary preference of many zooplankton (Sterner 1989) and it is easily measured. I used 35 μm as a size-based cut-off between highly edible and grazer-resistant algae (hereafter referred to as "inedible" algae for simplicity). This choice was based on known size preferences of filter-feeding Cladocera (Sterner 1989) and has been used in previous studies as an effective proxy measure of edibility (Carpenter et al. 1987, Sarnelle 1992, Cottingham 1999). One sub-sample was first filtered through a 35 μm mesh and then filtered onto a Whatman GF/F filter (Whatman Inc., Ann Arbor, Michigan, USA). The other sub-sample was filtered onto a GF/F filter in totality to measure total algal standing crop. All filters were frozen and later analyzed for chlorophyll *a* using narrowband fluorometry (Welschmeyer 1994) as a measure of algal biomass.

Following algal collection, each enclosure was gently mixed and a 1 l water sample obtained using a hand pitcher. Zooplankton were then extracted by filtering through 80 μm mesh, preserved in acid Lugol's solution, and the water was returned to the enclosure. Zooplankton samples were later counted in totality. This procedure was repeated for $-Z$ treatments to monitor for zooplankton invaders and to ensure that all enclosures received the same amount of mixing. A day following sampling, wall growth was removed by scrubbing enclosure walls with a brush, and well water was added to counter evaporative and sampling losses. To minimize cross contamination, separate sampling gear was used for all treatment combinations and gear was thoroughly rinsed with well water between enclosure samplings. On the final sample date, additional water samples were taken and replicates of each treatment

pooled to create one 800 ml sample for each treatment combination. These were preserved with acid Lugol's solution and later used to examine algal composition after settling. Algae were generally identified to the genus level. A random sub-set of individuals of each taxon was also measured to obtain estimates of mean size per taxon (based on greatest linear distance).

Phytoplankton and zooplankton responses were $\log_{10}$ transformed and relative abundance data were arcsine-square root transformed to achieve homogeneity of variances. Responses were analyzed using univariate repeated measures ANOVA (rm-ANOVA). Due to potential violations of the assumption of circularity, Greenhouse-Geiser adjusted probabilities are presented for all within subjects effects. *Ceriodaphnia* failed to establish in one $+Z+N$ replicate, and mid-experiment the rotifer *Monostyla* was detected in one $-Z+N$ replicate; these have been removed from all analyses and graphical depictions. Furthermore, *Chaoborus* (a planktivorous midge larvae) was detected in one $+Z+N$ replicate on day 71, driving *Ceriodaphnia* densities below limits of detection. This replicate, on day 71, was also removed from analyses and figures. All statistics were performed using Systat Version 8.0.

Four days after the final sample date, I performed a series of experiments in order to quantify trade-offs among varying size classes of algae present in the experimental enclosures. I focused first on edibility by performing feeding trials with *Ceriodaphnia*. Seston was collected from the enclosures (excepting aforementioned replicates that were excluded) and pooled. *Ceriodaphnia* were removed using carbonated water and by decanting (see aforementioned methodology) and the water was aerated. *Ceriodaphnia* for the assay were isolated from cultures and then placed in well water without food for approximately 2 hours (only adults between 0.7 and 0.9 mm were used). At the initiation of the experiment, *Ceriodaphnia* were randomly distributed to ten 250 ml beakers with a small volume of well water (25 individuals per beaker); ten control beakers received an equal amount of zooplankton-free well water. Seston was then added (200 ml per beaker) and beakers were placed on a shaker table at 150 rpm in the dark at 22°C. After 9 hours, *Ceriodaphnia* were removed and grazing beakers were randomly divided into two groups of five and then pooled to create two "replicate" samples. The same was done for controls to create two "replicates." Pooling was required to obtain adequate sample volumes for chlorophyll *a* analyses. No zooplankton mortality was detected. To examine different size classes of algae, water samples were first filtered through mesh screens then onto GF/F filters for chlorophyll *a* analysis. I used four mesh sizes to examine five size fractions (<35, 35–60, 60–80, 80–250, and >250 μm). Assuming all beakers started with the same initial algal assemblage, I calculated a grazing rate for each size fraction as $[(\ln N_c - \ln N_z)/t] \times (V/N)$ (Knisely and Geller 1986), where N_z was the mean final chlorophyll *a* concentration in the presence of zooplankton, N_c was the mean final concentration in controls, V was the sample volume in ml, N was the number of grazers, and t was the duration of the trial (9 hours).

Two days following grazing assays, algal growth experiments were performed. Seston was collected from experimental enclosures and zooplankton were removed using the aforementioned protocol. Water was divided evenly among eighteen 250 ml beakers (200 ml of water each). Twelve beakers received an addition of 200 μg phosphorus l^{-1} (as KH_2PO_4), plus nitrogen (as NH_4NO_3) in a 17:1, N:P molar ratio. Six control beakers received no additions. Beakers were then placed on a shaker table at 150 rpm under fluorescent light fixtures. After 46.5 hours, the experiment was terminated and beakers were randomly pooled to create two 600 ml control "replicates" and four 600 ml nutrient addition "replicates." Protocols for water fractionation matched those of the grazer assay. I calculated for each size fraction an algal growth rate as $[\ln(N_n) - \ln(N_c)]/t$, where N_n was the mean final chlorophyll concentration with nutrients, N_c was the mean final concentration in controls, and t was the duration (46.5 hours). Time durations for both grazer and nutrient assays were based on pilot experiments performed prior to the assays. Both grazing and algal growth rates for all size fractions were determined to be constant over these time intervals.

Results

Block effects were not detected and have been removed from the following analyses. Nutrient enrichment successfully enhanced productivity, as suggested by both zooplankton density and total chlorophyll *a* levels (Fig. 1 and 2). *Ceriodaphnia* responded positively ($p < 0.001$, $F_{1,4} = 106.81$, between subjects effect, rm-ANOVA), as did algal biomass ($p < 0.00001$, $F_{1,9} = 87.89$, between subjects effect, rm-ANOVA).

To explore grazer-nutrient effects on phytoplankton, I restricted analyses to days 22–71. This corresponds to the period after which *Ceriodaphnia* had responded numerically to enclosure conditions and thus more accurately reflects the assumptions of the keystone model. *Ceriodaphnia* had effects on chlorophyll *a* levels, but results depended on the level of nutrient enrichment (Fig. 2). When comparing $+Z-N$ treatments to $-Z-N$ controls, grazer effects were relatively weak at this low level of enrichment. In contrast, *Ceriodaphnia* presence had a strong positive effect on total chlorophyll *a* in high nutrient treatments. Though a between subjects main effect of *Ceriodaphnia* presence was not detected ($p = 0.25$, rm-ANOVA), there was a significant

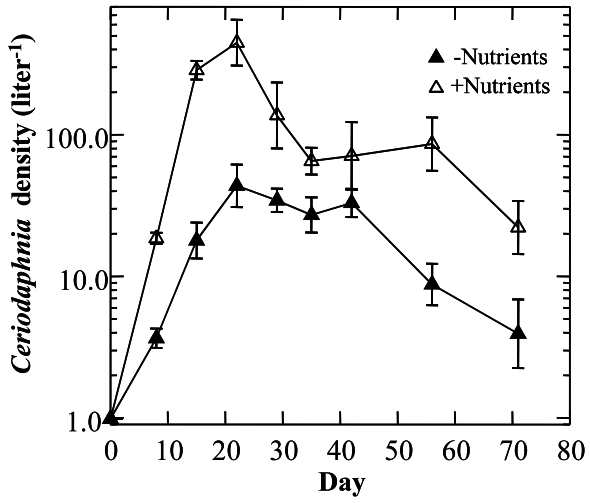


Fig. 1. Effects of nutrient enrichment on *Ceriodaphnia* density through time. Shown are means (± 1 S.E.).

nutrient × grazer interaction ($p < 0.01$, $F_{1,9} = 13.41$, between subjects effect, rm-ANOVA).

Focusing on the edible size fraction of algae first, when averaged over the experimental period, edible chlorophyll *a* responded positively to enrichment (Fig. 3A; $p < 0.001$, $F_{1,9} = 47.05$, between subjects effect, rm-ANOVA). While no between subjects grazer effects were detected ($p > 0.10$), interactive effects with enrichment level were detected through time (time × nutrient × grazer effect, $p < 0.001$, $F_{5,45} = 9.93$, rm-ANOVA). Early in the experiment (days 22 and 29), grazers had significant negative effects on edible algae

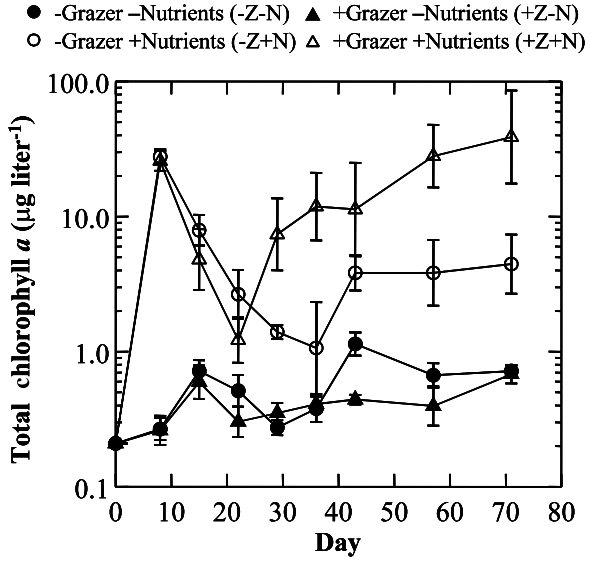
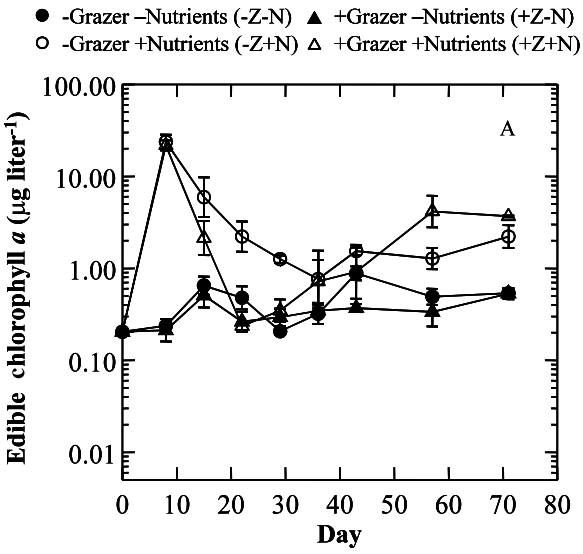


Fig. 2. Mean total chlorophyll *a* responses through time in the presence and absence of grazers and at low or high nutrient enrichment (± 1 S.E.). Day 0 values are based on sub-samples of algal inocula.



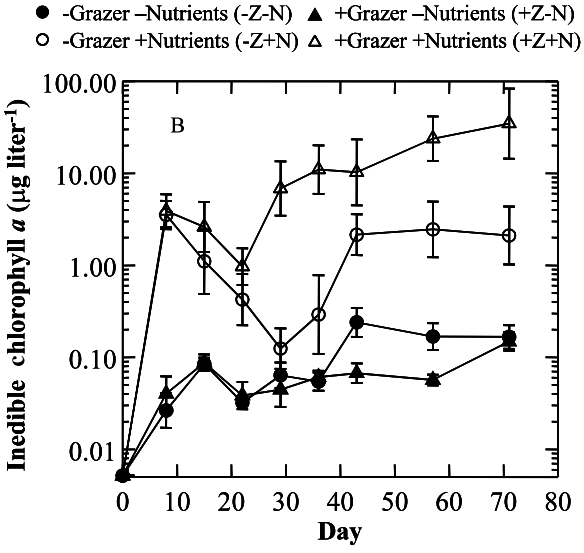


Fig. 3. Effects of nutrient enrichment and grazer presence/absence on A) edible (< 35 μm) chlorophyll *a* and B) inedible (> 35 μm) chlorophyll *a*. Means (± 1 S.E.). Day 0 values are based on sub-samples of algal inocula.

in + N treatments (Fig. 3A; $p < 0.05$, ANOVA). By day 57, the direction of the effect had switched to a positive one. No grazer effects were detected on day 71 ($p > 0.05$, ANOVA). Inedible algal biomass was determined by subtracting edible (< 35 μm) chlorophyll *a* from total chlorophyll *a* measures. Overall patterns of the inedible fraction largely mirrored total chlorophyll *a* responses (Fig. 3B). Inedible algae responded to nutrient enrichment ($p < 0.001$, $F_{1,9} = 38.26$, rm-ANOVA) but the magnitude of this effect was higher in the presence of *Ceriodaphnia* (Fig. 3B), evidenced by a significant grazer × nutrient interaction ($p < 0.001$, $F_{1,9} = 33.78$, between subjects effect, rm-ANOVA). Fi-

nally, I detected interactive effects of grazers and nutrient enrichment on the relative biomass of inedible algae (calculated as inedible chlorophyll *a* divided by total chlorophyll *a*). Though inedible algae were generally favored by enrichment ($p = 0.001$, $F_{1,9} = 22.47$, between subjects effect, rm-ANOVA), dominance by inedible forms was much stronger in the presence of grazers (Fig. 4); a main effect of *Ceriodaphnia* was not detected ($p = 0.24$) but a significant interaction between nutrient enrichment and grazers was present ($p < 0.001$, $F_{1,9} = 59.83$).

Examination of pooled algal samples (obtained at the end of the experiment) showed that inedible forms in $+Z+N$ treatments were dominated by filamentous green algae (*Mougeotia*) and filamentous cyanobacteria (*Oscillatoria*, *Cylindrospermum* and *Microcoleus*). Present, but at much lower densities, were large (>50 μm) diatoms (e.g. *Synedra*). These same groups dominated the inedible fraction in $-Z+N$ treatments as well. Gelatinous and digestion-resistant taxa were not observed in any of the treatments.

In lab assays, smaller size classes of algae were more susceptible to consumption by *Ceriodaphnia* (Fig. 5A). Only grazing rates for the <35 and 35–60 μm fractions were significantly different from zero ($p < 0.05$, bootstrapped t-tests). The grazing rate for the 35–60 μm size class was also significantly higher than the <35 μm fraction ($p < 0.05$, bootstrapped t-test). In the algal growth experiment, positive growth rates were detected for all size classes of algae but the three smallest size fractions displayed higher rates compared to the two large size classes (Fig. 5B). Rates among the

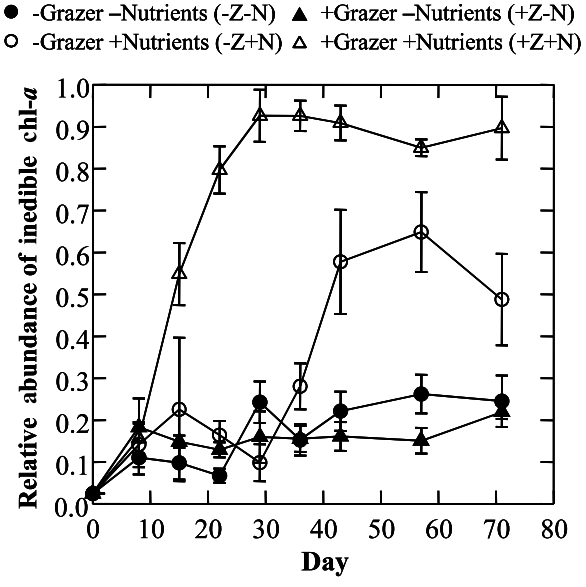


Fig. 4. Effects of nutrient enrichment and grazer presence/absence on mean relative abundance of inedible chlorophyll *a* through time (±1 S.E.).

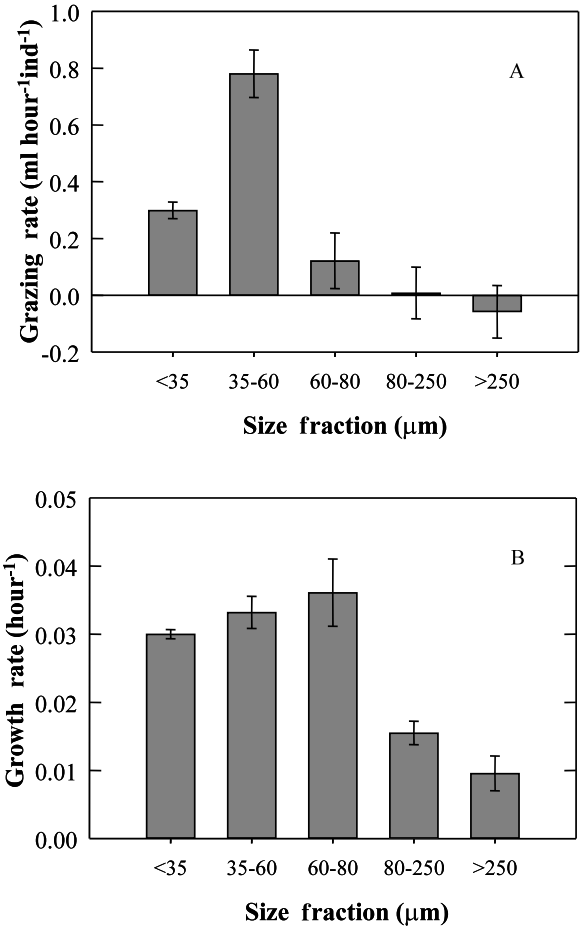


Fig. 5. Results of algal growth and grazing assays. A) Per capita grazing rates of *Ceriodaphnia* on five size fractions of algae. B) Per capita growth rates of each size fraction of algae in response to enrichment and in the absence of grazers. Shown are means with bootstrapped standard error bars.

<35, 35–60, and 60–80 μm fractions were not significantly different from each other ($p > 0.50$, Bonferroni adjusted, bootstrapped t-tests). However, growth rates for these three size classes were all significantly higher than the 80–250 and >250 μm fractions (all $p < 0.05$, Bonferroni adjusted, bootstrapped t-tests).

Discussion

When first articulated, keystone predation embodied a bold proposition for its time; the importance of predators as regulators of community structure was still not wholly accepted (Peet 1991). Though the contributions of Paine (1966) and Brooks and Dodson (1965) are now firmly entombed in textbooks, the role that consumers play, relative to bottom-up forces, in generating trophic structure remains controversial (Strong 1992, Polis and Strong 1996). A mutual increase in the biomass of all

trophic levels to increasing productivity is commonly interpreted as evidence of strong bottom-up control and weak predator effects (Arditi and Ginzburg 1989); the preponderance of this pattern in nature could thus be taken as a broader indictment of the role of predation. Yet, the keystone model demonstrates that predators may still be central to such patterns through the facilitative effects they have on prey composition and turnover. Thus, both bottom-up and top-down forces may act concomitantly to generate observed trophic structures.

There are several studies that have revealed keystone effects on species composition and diversity (Paine 1966, Levin et al. 1977, Lubchenco 1978, McCauley and Briand 1979, Hillebrand et al. 2000). However, experimental evidence of the interactive effects of predation and productivity on prey composition and trophic-level biomass involving multiple generations of predator and prey has been less available (though see Bohannan and Lenski 1999, 2000). My experiment provided some support for the keystone predator model. The presence of grazers clearly facilitated shifts in dominance to larger (presumably less edible) species of phytoplankton. As predicted, this shift was only evident when nutrient levels were high. At low enrichment levels, biomass and size structure of algae were very similar regardless of grazer presence or absence. This supports the contention that consumer and resource effects can act in concert, in an interactive manner, to influence the composition and total biomass of prey assemblages. These results complement previous studies that have revealed effects of within trophic-level heterogeneity on consumer-resource effects (Hansson et al. 1998, Persson et al. 2001, Steiner 2001) and the work of Bohannan and Lenski (1999, 2000), in which keystone predator effects were revealed in microbial systems.

At its core, the keystone model assumes that the ability to compete for limiting resources comes at a price – a greater vulnerability to predation. The mechanistic basis of this trade-off can be highly varied (having a behavioral, morphological or physiological basis). Though there are several traits that may determine edibility among planktonic algae (e.g. gelatinous sheathing or toxicity), size may be vital to determining both competitive ability and susceptibility to grazing by filter feeding zooplankton (Sterner 1989). Smaller size can confer a growth advantage over larger size classes of algae, at least at high levels of nutrient resources as shown by the algal growth assay. This could translate into a longer-term competitive advantage as resources become limiting in the environment. Yet, *Ceriodaphnia* fed most effectively on these smaller, rapid growth forms. Thus, my results offered support for a size-based keystone trade-off, though admittedly the relationship between growth rate, grazing rate, and size was not tightly coupled. This was likely due, in part, to my use of broad size classes of algae; by doing so I gained ease of measurement at the cost of resolution. A point of concern is that the keystone predator model bases competitive ability on the minimal resource level required to maintain zero net population growth (i.e. $R \times s$; Leibold 1996). Short-term growth responses may not reflect performance at equilibrium, especially if algal species display trade-offs in their ability to grow at high versus low nutrient levels. Hence, some caution is warranted when interpreting the growth experiment. Another point to consider is that small size does not invariably increase vulnerability to grazers; some algae possess gelatinous sheaths or cell structures that allow them to avoid digestion by zooplankton (Sterner 1989). Furthermore, nutrient limitation is known to affect the cell walls of some taxa, decreasing digestibility and permitting viable gut passage (Van Donk et al. 1997). Such effects would not be revealed in short-term feeding trials. Known gelatinous and digestion-resistant taxa were not observed in my experiment. However, it is possible that nutrient limitation may have increased digestion resistance of some small taxa in low nutrient enclosures, potentially rendering a simple size-based measure of edibility somewhat questionable. Hence, the reader should bear this caution in mind when interpreting my results. Finally, grazers obtained their highest feeding rates on the 35–60 μm fraction, suggesting that a 35 μm cut-off between edible and inedible algae may have over estimated the inedible fraction. This was unlikely since the majority of phytoplankton in the inedible size class were filamentous species, taxa with sizes much greater than 60 μm.

My experiment did produce some unexpected results. Total biomass of algae was actually higher in the presence of zooplankton in high nutrient treatments compared to $-Z+N$ controls. This was almost entirely due to the positive response of inedible algae. Though algal biomass was expected to increase in response to enrichment, the keystone model predicts that prey biomass should be lower in the presence of top-consumers. Furthermore, I predicted that small edible algae (being more efficient resource competitors) would dominate at both nutrient levels, in the absence of grazers. Instead, inedible forms persisted and at times co-dominated in the $-Z+N$ treatment. There are several mechanisms that may account for these results. First, inedible algae were composed primarily of filamentous taxa (cyanobacteria and green algae) that grew suspended in the water column and in a film on the water surface. This may have conferred two advantages. First, filamentous algal mats may have shaded the water column, creating competition for light. Second, because enclosures were rarely mixed, sedimentation was likely an important source of mortality for algae (Reynolds 1984). The ability to remain suspended in the water column would have freed filamentous taxa from this mortality source. These factors may account

for the ability of filamentous forms to persist, even in the absence of the facilitative effects of grazers, and may also explain the continued dominance of filamentous algae in $+Z+N$ treatments, despite drops in *Ceriodaphnia* densities mid-experiment. Finally, because of low mixing rates, nutrients may have become increasingly bound in bottom sediments as the experiment progressed. Consequently, nutrient recycling by grazers may have been an important source of limiting nutrients in the water column. Hence, filamentous algae may have received this added benefit in $+Z+N$ treatments allowing it to attain exceptionally high biomass levels.

A point of concern is whether these hypothesized processes were purely artifacts of the experimental system. Although my enclosures likely enhanced effects due to high water-surface to volume ratio and infrequent mixing, similar mechanisms are commonly observed in natural systems. For example, zooplankton are thought to be an important regenerative source of dissolved nitrogen and phosphorus in stratified lakes, potentially counter-balancing grazing effects on algae (Lehman 1980, Moegenburg and Vanni 1991). Furthermore, buoyancy is known to be an important mechanism counteracting algal sedimentation losses (Reynolds 1989), and filamentous cyanobacteria commonly form surface scums in eutrophied systems, shading out competing algae (Paerl 1988). Gragnani et al. (1999) have explored this dynamic mathematically, examining the interaction between grazers, edible algae and filamentous cyanobacteria with combined nutrient and light competition. Though they do not provide an analysis of trophic-level biomass in their study, they show that grazers can mediate co-existence between these two algal groups as well as facilitate dominance by inedible cyanobacteria, in accordance with the keystone model. However, they further demonstrate that filamentous taxa can also dominate even in the absence of grazers at high nutrient levels due to light competition. This occurs because filamentous forms enhance light attenuation (i.e. increase turbidity) but are also better light competitors, thereby reinforcing their own dominance through positive feedback (Scheffer et al. 1997). These results combined with my findings suggest that the mechanisms underlying the generation of algal size structure in nature likely reach beyond the simplistic keystone framework, being the product of the interactive effects of zooplankton grazing and nutrient recycling, mixing regime, light competition, and competition for shared nutrients.

Heterogeneity within trophic levels can take many shapes, but a common form is the trait variation that can occur among species in their abilities to obtain resources and avoid predators (i.e. variation in interaction strength among species). Accounting for this variation implicitly requires us to approach communities not as linear food chains, but as food webs. By integrating such complexities in an explicit fashion, it is possible to gain a broader understanding of how individual species deal with and respond to their environments. The idea that heterogeneity among species within trophic levels can have consequences for community responses to bottom-up and top-down forces is not new. In the past, a common view was that prey heterogeneity and the reticulate nature of food webs could render predators ineffective. Yet, the keystone model shows that predation can be a vital component of prey responses to resource effects within food webs. Though many other complexities clearly operate in nature, keystone effects may be an important ingredient in the regulation of trophic-level biomass in planktonic communities.

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