

Nonlinear Effects of an Aquatic Consumer: Causes and Consequences

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ABSTRACT: The assumption that per capita consumer effects on prey density are independent of consumer and prey density is examined with a large-scale manipulation of an aquatic herbivore (*Daphnia*). A gradient of consumer removal was maintained long enough to allow the abundances of both consumer and prey (phytoplankton) to equilibrate to the manipulation. Strong and unequivocal nonlinearities were found in the effect of *Daphnia* on total phytoplankton abundance and the abundance of most of the common phytoplankton species. *Daphnia*'s suppression of phytoplankton was strong between 0 and $\sim 400 \mu\text{g } Daphnia \text{ L}^{-1}$ but essentially nil from ~ 400 to $900 \mu\text{g } Daphnia \text{ L}^{-1}$. The sharp deceleration in *Daphnia*'s effect was not caused by a shift within the phytoplankton community toward consumption-resistant forms. The most likely explanation for the deceleration was a reduction in *Daphnia*'s filtering effort at low phytoplankton abundance, that is, a Type III functional response. A review of experimental literature suggested that decelerating effects of consumers are the norm in aquatic systems. Nonlinear effects present problems for the estimation of interaction strength and the building of community interaction models from the results of predator manipulations. It is suggested that the role of field experiments in community ecology should be to test rather than to parameterize models.

Keywords: nonlinear effects, predation, herbivory, functional response, interaction strength, *Daphnia*, phytoplankton.

Most research into food web effects on community and ecosystem properties has focused on comparisons of systems having discrete differences in trophic structure. A common theoretical approach describes the response to enrichment of systems with different numbers of trophic levels (Hairston et al. 1960; Smith 1969; Abrams 1993a)

or systems in which trophic levels are added stepwise with enrichment (Oksanen et al. 1981; Holt et al. 1994). Both correlational and experimental studies commonly describe the response of ecosystems with different numbers of trophic levels to applied or natural gradients of enrichment (Leibold and Wilbur 1992; Sarnelle 1992b; Mazumder 1994; Mikola and Setälä 1998; Carpenter et al. 2001; Persson et al. 2001). Large-scale field experiments typically apply "sledgehammer" manipulations of food web structure (e.g., zero vs. high densities of zooplanktivorous fish) in an effort to push systems to their natural extremes (Crowder et al. 1988; Kitchell et al. 1988) and maximize the probability that effects will be detected statistically. The drawback of these approaches is that no information is obtained about intermediate states of the system. For example, it is likely that lakes vary widely in the degree to which piscivorous versus zooplanktivorous fish dominate, even across lakes with similar productivities (Carpenter et al. 1987), so we should expect gradients in nature in the amount of top-down predation pressure. Empirical efforts to date, however, have almost exclusively relied on comparisons of systems with or without one or another type of predator (Sarnelle 1992b; Brett and Goldman 1996, 1997; Schmitz et al. 2000).

Lack of information about how prey density responds to consumer gradients (rather than to consumer presence/absence) is also a major source of uncertainty with respect to the goal of linking species manipulations to dynamic food web theory. It has recently been suggested that experimental results be viewed in a broader theoretical context by operationalizing the concept of interaction strength (Osenberg et al. 1997; Laska and Wootton 1998). These articles have attempted to link the magnitude of a consumer's effect on prey density to theoretical constructs of interaction strength gleaned from simple food web models. However, the supposition that interaction strength is a simple parameter that can be measured with field manipulations of consumer presence/absence is perhaps naive (Bender et al. 1984; Abrams 2001). At the most basic level, arguments against the application of experimental effect size to the parameterization of food web or community-

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matrix models challenge the notion that consumer effects are likely to be linear (i.e., the per capita effect of consumers on the prey population is independent of consumer and prey density). Although critical to the application of interaction strength as a link between field experiments and dynamic theory, direct tests of the assumption of linear consumer effects are exceedingly rare (Abrams 1993*b*, 2001). Most field manipulations employ two (presence/absence) or a very few treatment densities of the consumer and are thus unsuitable for testing this assumption.

Consumer effects are often assumed to be linear (Freedman 1987; Yodzis 1989) despite much research and intuition about mechanisms that can introduce nonlinearity into consumer effects (Lehman 1976; Werner et al. 1983; Cooper 1984; Sih 1984; Lima and Dill 1990; Turner and Mittelbach 1990; Abrams 1993*b*; Werner and Anholt 1993; Kratz 1996). Considerable research has accumulated regarding the antipredator behavior of animal prey and the implications of that behavior for predator-prey interactions (e.g., Anholt and Werner 1999). For example, as predator density increases, animal prey are expected to spend more time in refuge, which may reduce the fitness of both predator and prey (Abrams 1993*b*; Anholt and Werner 1998). Most plants do not have behavior per se (although motile phytoplankton are an exception) but may respond to increased herbivory with chemical and structural defenses (Agrawal and Karban 1999; Berenbaum and Zangerl 1999; van Donk et al. 1999). Although the study of antipredator behavior and inducible defenses is well developed, the consequences of these phenomena for the functional relationship between consumer and prey density in nature have rarely been studied experimentally (Abrams 1993*b*; Diehl et al. 2000). Alternatively, consumers may, via selective grazing, shift prey populations or prey assemblages toward dominance by consumption-resistant forms, which would lead to a weakening of consumer effects at high consumer densities. A shift toward consumption-resistant species at high consumer densities is a cornerstone of keystone predation theory (Vance 1978; Holt et al. 1994; Leibold 1996), but there appear to be no experimental studies that explicitly examine the role of this shift in producing nonlinear effects of consumers on prey density in nature.

The primary objective of this article is to describe the results of a large-scale consumer-gradient manipulation demonstrating that strong nonlinearities exist in a simple consumer-prey interaction. Ancillary to this objective, I ask more generally whether existing experimental evidence indicates that nonlinear consumer effects are common or rare. The second major objective is to evaluate alternative mechanisms that could explain the nonlinear consumer effects I observed, with particular attention to the role of

consumer-mediated shifts in the consumption resistance of the prey.

The herbivore-phytoplankton interaction in lakes has certain advantages for the study of consumer-prey interactions, including rapid generation times, the general applicability of experimental results from large enclosures to nature (Mazumder et al. 1990; Sarnelle 1997), and the extensive background information available about mechanisms underlying the net effects of the herbivore (DeMott 1989; Sterner 1989). In addition, it is widely accepted that *Daphnia* is a key species in the food webs of lakes, with strong dynamic links to trophic levels both above and below (Brooks and Dodson 1965; Leibold 1989; Shapiro 1990; Carpenter et al. 2001). Thus, delineating the functional form of the response of phytoplankton to top-down variation in *Daphnia* abundance should help to clarify our understanding of this important food web linkage.

Although several studies have examined phytoplankton responses across an experimental herbivore gradient (e.g., Lehman and Sandgren 1985; McCauley and Kalff 1987; Elser and MacKay 1989; Elser et al. 1990), these studies have typically been of short duration (≤ 7 d), such that herbivore density could be assumed to approximate a fixed parameter. In contrast, the field experiment described in this article focuses on the response of phytoplankton to a herbivore removal gradient that was maintained long enough to allow both phytoplankton and herbivore density to equilibrate demographically to the manipulation. In general, field experiments of the latter type are exceedingly rare in the study of consumer-prey interactions (see Leibold and Tessier 1998 for a previous example in lakes).

Expectations

To clarify how different mechanisms may produce nonlinearities in phytoplankton response, it is useful to generate expectations about experimental results using a simple model. One such model (McCauley et al. 1988) is

$$\begin{aligned}\frac{dA}{dt} &= rA\left(1 - \frac{A}{K}\right) - f_g(A)AD, \\ \frac{dD}{dt} &= cf_g(A)AD - dD,\end{aligned}$$

where A is phytoplankton biomass, D is *Daphnia* biomass, r is maximum phytoplankton growth rate, K is maximum phytoplankton biomass (carrying capacity), c is the proportion of ingested phytoplankton that is converted into new *Daphnia*, d is *Daphnia* mortality, and $f_g(A)$ is a function describing *Daphnia* feeding on phytoplankton. In this type of model, *Daphnia* biomass is a dynamic variable as

well as the ultimate target of experimental manipulation. To examine the functional form of the net effect of *Daphnia* on phytoplankton in this model, *Daphnia*'s death rate (d) is varied, and the ensuing relationship between phytoplankton biomass and *Daphnia* biomass at equilibrium is examined. This approach contrasts with models that treat herbivore abundance as a fixed parameter (Sterner 1989), which are more suited to experiments that last only a few days (Lehman and Sandgren 1985; McCauley and Kalff 1987). The model described here is more appropriate for experiments in which a *Daphnia* gradient is maintained by varying the rate of experimental *Daphnia* removal or for average conditions during the growth season in lakes that differ in the amount of predation pressure on *Daphnia* (Sarnelle 1992b, 1999; Mazumder 1994; Leibold and Tessier 1998; Carpenter et al. 2001).

In a Lotka-Volterra model of this type, the relationship between consumer and prey abundance is typically negative when plotted across all biologically possible herbivore death rates. Our interest here is in the shape of this negative relationship, which is determined by the nature of the feeding function ($f_g(A)$). For simplicity, I generated three contrasting predictions about the shape of the response of phytoplankton to an experimental *Daphnia* gradient by assuming that either *Daphnia*'s feeding function takes the form of a constant attack rate (i.e., constant instantaneous mortality inflicted by each *Daphnia*) or attack rate increases or decreases with phytoplankton density. If *Daphnia* has a constant attack rate, then the response of phytoplankton biomass to a *Daphnia* biomass gradient at equilibrium is negative and linear. To examine the other two cases, I let *Daphnia*'s feeding rate take the form of a Type II (attack rate decreases with prey density) or Type III (attack rate increases with prey density at low prey densities) functional response. These familiar functional responses provide a simple, phenomenological way of looking at how changes in attack rate affect the relationship between consumer and prey abundance across a consumer death rate gradient.

For the model with a Type II functional response, there is generally a range of low *Daphnia* death rates over which equilibrium *Daphnia* biomass increases slightly with increasing death rate (and as a consequence, *Daphnia* and phytoplankton biomass are positively related). To simulate the outcome of a *Daphnia* removal experiment for this case, I limited the analysis to higher death rates over which *Daphnia* biomass declined monotonically with increasing death rate. This model predicts an accelerating negative relationship between *Daphnia* and phytoplankton biomass (fig. 1A); that is, *Daphnia*'s effect strengthens with increasing *Daphnia* density. For the model with a Type III functional response, there is a range of phytoplankton biomass over which *Daphnia*'s attack rate declines rather than

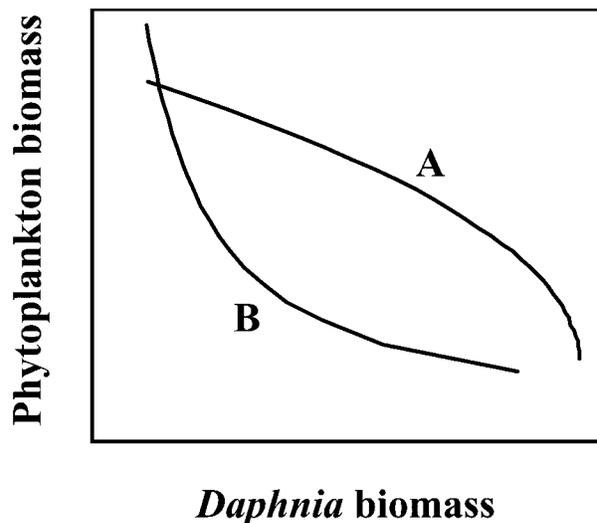


Figure 1: Expected functional relationships between consumer (*Daphnia*) and prey (phytoplankton) density at equilibrium for simple predator-prey models. A, Type II functional response. B, Type III functional response. Model parameters were the same in each case, except for the range of consumer death rates used to generate the graphs.

increases with phytoplankton, since the standard Type III formulation (Gotelli 1998) includes feeding-rate saturation at high prey densities. In this case, I limited the analysis to a range of phytoplankton biomass over which *Daphnia*'s attack rate increased monotonically with increasing phytoplankton. In this case, the model predicts that the strength of *Daphnia*'s effect will decrease as *Daphnia* density increases (fig. 1B).

Several mechanisms can result in changes in attack rate with prey density and so lead to nonlinear functional relationships, and there is laboratory evidence suggesting that many of these mechanisms operate over some range of *Daphnia* or phytoplankton density. For example, an increase in *Daphnia*'s attack rate as phytoplankton decreases may simply result from saturation of *Daphnia*'s feeding rate at high phytoplankton densities. Classic laboratory studies of *Daphnia* feeding have concluded that *Daphnia* feeds with a Type II functional response (DeMott 1982; Porter et al. 1982). An alternative mechanism (absent from the above models) that could produce an accelerating negative effect of *Daphnia* on phytoplankton (fig. 1A) is a function of the positive effect of nutrient excretion by *Daphnia* on phytoplankton division rate (Sterner 1986; Elser 1992). In this case, increase in the strength of *Daphnia*'s net effect with increasing *Daphnia* density results from saturation of the phytoplankton growth response to herbivore-supplied nutrients at high levels of nutrient availability (see Sterner 1989).

Several mechanisms can lead to a decrease in *Daphnia*'s attack rate as *Daphnia* increases (fig. 1B). For example, *Daphnia* might reduce its foraging effort at low food levels (Plath 1998, 1999) or exhibit self-limitation of feeding at high densities (Hayward and Gallup 1976; Helgen 1987; Matveev 1993). Alternatively, intense grazing at high *Daphnia* density may result in the phytoplankton becoming more resistant to herbivory via shifts in phytoplankton species composition (Porter 1977; Leibold 1989; Leibold et al. 1997), induced morphological or chemical defenses within phytoplankton species (van Donk et al. 1999), or the presence of a spatial refuge where phytoplankton can escape predation (Scheffer and Rinaldi 2000). Increased resistance to herbivory would, in effect, reduce the per capita grazing mortality inflicted by individual *Daphnia*.

Methods

The experiments were conducted in Zaca Lake, a naturally eutrophic lake in southern California. The lake is thermally stratified for much of the year, leading to persistent anoxia in the deep waters. Total phosphorus concentrations in the mixed layer average about $300 \mu\text{g L}^{-1}$ during winter mixing periods and range from 50 to $250 \mu\text{g L}^{-1}$ during stratified periods (Sarnelle 1992a), making the lake extremely productive. The lower limit of the mixed layer generally resides between 4 and 6 m. One of my earlier works (Sarnelle 1993) provides a more detailed description of the lake.

Large-Scale Enclosure Experiment: The Net Effects of Daphnia on Phytoplankton

Twelve large tubular enclosures made of clear polyethylene sheeting (diameter, 2.3 m; depth, 8 m) were deployed in the middle of Zaca Lake on April 17, 1994. Each enclosure was fitted with coarse netting on the bottom to exclude fish but not zooplankton, when the enclosure bottom was lowered. Otherwise, enclosure bottoms were open to the anoxic hypolimnion, which prevented immigration/emigration by plankton. Enclosures were open to the atmosphere at the top, suspended from rafts, and held open by attaching a weight to a PVC hoop attached to the bottom edge of the polyethylene tube. As a result of the deployment protocol and natural zooplankton patchiness, *Daphnia* abundance varied substantially among enclosures before the manipulation was initiated (range, $50\text{--}400 \mu\text{g L}^{-1}$).

Enclosures were manipulated by slowly pulling a large zooplankton net (diameter, 1 m; mesh, $250 \mu\text{m}$) through each enclosure every 3–4 d. The objective of the manipulation was to create a gradient of *Daphnia* removal rather than to manipulate all planktonic herbivores. The same number of net hauls was made in every enclosure to con-

trol for mixing effects, whereas the gradient of *Daphnia* removal was established by varying the number of times the contents of each net haul was either removed from the enclosure (ranging from 0 to 13 times per week) or emptied back into the enclosure (sham hauls, no zooplankton removed). Zooplankton collected in sham hauls were released back into the enclosure without lifting the net out of the water. As a test of the direct effect of removal on zooplankton species abundance, I sampled zooplankton immediately before and after making four removal hauls in each of three enclosures. Only the abundance of *Daphnia* was significantly reduced in this test (one-tailed *t*-test, $P < .05$).

The enclosures were sampled twice weekly for phytoplankton and zooplankton. Depth-integrated samples for phytoplankton and small zooplankton (rotifers) were taken from the euphotic zone with a tube sampler (51-mm inside diameter). Phytoplankton and rotifers were preserved in Lugol's solution and formaldehyde, respectively. Rotifer biomass was negligible in all enclosures ($<1 \mu\text{g L}^{-1}$ dry biomass) throughout the study, so these data were not analyzed further. Phytoplankton species abundances were estimated with the inverted microscope technique (see Sarnelle 1993 for details) and expressed as dry biomass ($\mu\text{g L}^{-1}$), which was calculated from measures of cell volume, assuming that phytoplankton have a specific gravity of 1 and a dry : wet mass ratio of 0.10. Total phytoplankton biomass as chlorophyll *a* was estimated weekly by extracting seston collected on Gelman A/E filters in 90% ethanol, followed by spectrophotometric analysis without acid correction (Sartory and Grobbelaar 1984). Total phytoplankton carbon was estimated by assuming a chlorophyll : carbon ratio of 0.033 (Reinertsen et al. 1990).

Nutrient concentrations were monitored weekly from depth-integrated water samples taken with the tube sampler. The organic carbon content of seston in two size fractions ($1\text{--}149 \mu\text{m}$ and $1\text{--}35 \mu\text{m}$) was measured by passing lake water through the appropriate sieves and collecting size fractions on a Gelman A/E filter (nominal pore size = $1 \mu\text{m}$). Seston carbon on the filters was measured with a CHN analyzer (Control Equipment model 240XA). The $1\text{--}35\text{-}\mu\text{m}$ size class roughly corresponds to the most edible fraction of seston for planktonic herbivores (Watson and McCauley 1988). Orthophosphate (SRP), total phosphorus (TP), and particulate phosphorus ($1\text{--}35\text{-}\mu\text{m}$ fraction) were analyzed via standard spectrophotometric techniques (Sarnelle 1999).

Macrozooplankton (crustaceans) were sampled with vertical hauls of a 13-cm diameter, $102\text{-}\mu\text{m}$ mesh net, which was assumed to have an efficiency of 60% on the basis of previous empirical experience (Sarnelle 1992a). Four net hauls from each enclosure were pooled into a single sample, and samples were preserved in sucrose for-

malin (Haney and Hall 1973). Zooplankton were counted and measured at $40\times$ in a Sedgwick-Rafter cell. Measurements of body length were made with a digitizer and drawing tube and used to calculate dry biomass using equations developed from dried Zaca Lake specimens. Zooplankton biomass (as $\mu\text{g L}^{-1}$) was calculated assuming that zooplankton populations inhabited depth strata that had measurable concentrations of dissolved oxygen. The depth of the water column inhabitable by zooplankton varied between 6.5 and 7.5 m across the enclosures and was not affected by the removal manipulation.

The functional relationship of interest is that between *Daphnia* biomass and phytoplankton biomass at equilibrium. I sought to maximize the fit of the experimental data to this ideal by choosing a sampling window extending from day 21 to day 32 of the experiment. Data from three phytoplankton (days 25, 28, 32) and four zooplankton (days 21, 25, 28, 32) samples were averaged and the averages used to examine the *Daphnia*-phytoplankton relationship. For variables measured once per week (chlorophyll, nutrients), I analyzed relationships between the variable on day 28 and average *Daphnia* biomass as described above. After day 32, the removal gradient was no longer sufficient to produce a clear gradient in *Daphnia* biomass, perhaps because of an increase in lake temperature and a consequent decrease in *Daphnia* generation time. I present zooplankton data for days 0–48 for the three enclosures with the lowest rates of removal to help assess whether *Daphnia* populations were near a long-term average during the days 21–32 window.

Phytoplankton Mortality Measurement

The large-enclosure experiment was designed to measure the net effect of *Daphnia* on the phytoplankton assemblage under natural conditions, and it potentially included both direct negative (via consumption) effects and indirect positive effects stemming from grazer excretion of dissolved nutrients (N and P), reduced algal uptake of nutrients, and increased light availability (Sterner 1986; Spencer and King 1989; Elser 1992). To isolate direct mortality effects and provide estimates of the relative grazing resistance of individual phytoplankton taxa, I conducted a short-term *Daphnia* manipulation on May 10–11, 1994. This experiment was conducted in the dark to prevent the phytoplankton from showing growth stimulation in response to grazer presence (Sarnelle 1993).

Phytoplankton were collected from the lake and from six of the large enclosures having widely divergent *Daphnia* densities, screened through 48- μm mesh (which effectively removed all but protozoan grazers), and pooled. The large enclosures developed contrasting algal communities in response to herbivore manipulation, so mortality rates of

many species could be determined simultaneously in a single incubation via this pooling technique. To maximize *Daphnia*'s filtering rates and reduce the impact of protozoan grazers (Landry and Hassett 1982), the pooled phytoplankton were diluted ($\sim 50 : 50$) with filtered lake water (1 μm nominal retention). *Daphnia* were collected from a high-*Daphnia* enclosure, concentrated with a 250- μm mesh sieve (to reduce densities of other crustaceans), and added to the diluted phytoplankton. The phytoplankton-*Daphnia* mixture was then dispensed into buckets. Two treatments were applied by sieving the water in three of the buckets through 250- μm mesh (control) while leaving four buckets unsieved (grazed). The contents of each bucket were then sampled for initial phytoplankton densities, poured into a 10-L polyethylene container (cubitainer), and incubated in the lake for 24 h. Cubitainers were enclosed in a double layer of black plastic during incubation, which reduced light availability by 99.99%.

At the end of the incubation, each cubitainer was sampled for final densities of phytoplankton and zooplankton. Instantaneous mortality rates (d^{-1}) for each phytoplankton species were determined as $\ln(C_i) - \ln(C_f)$, where C_i and C_f are initial and final phytoplankton cell densities, respectively. Mortality rates were corrected for changes in the controls, which were typically $< \pm 25\%$. One species, *Oocystis* sp., tended to increase in controls, so mortality rates calculated for this species could be suspect. However, inclusion of this species in subsequent analyses did not impact any results.

Results

Large-Scale Enclosure Experiment: The Net Effects of Daphnia on Phytoplankton

The manipulation created a gradient in *Daphnia* biomass across the large enclosures (fig. 2). It was not until day 11 of the experiment that the effect on *Daphnia* was statistically significant, and it was not until day 14 that the effect became large (slope of *Daphnia* biomass vs. number of removal hauls > -40), as seen during the sampling window (fig. 2). Whether considered over all days (5–32) or during the sampling window (21–32), time-averaged *Daphnia* biomass was significantly affected by the removal gradient (linear regression, $P < .005$), whereas none of the other common zooplankton taxa were affected ($P > .10$). *Daphnia pulicaria* was the dominant daphnid species, averaging $\sim 80\%$ of total *Daphnia* biomass over all but one enclosure, and there was no effect of the removal gradient on the distribution of biomass among the daphnid species present (linear regression, $P > .50$). In one enclosure (5.8 removals per week), *Daphnia* biomass comprised a mixture of three species (*D. pulicaria*, 26%; *Daphnia galeata*,

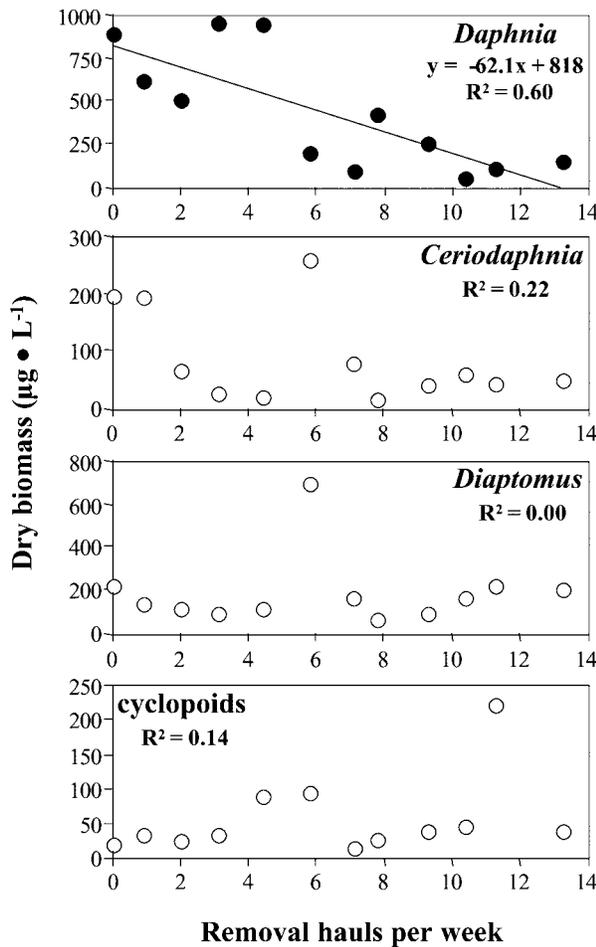


Figure 2: Effect of the removal manipulation on the biomass of common zooplankton taxa during the sampling window (days 21–32) of the enclosure experiment.

29%; *Daphnia parvula*, 45%), but this enclosure was not found to be exceptional in any subsequent analysis.

For the three enclosures with the lowest rates of removal, which were monitored for 48 d, average *Daphnia* biomass during the sampling window was reasonably representative of long-term average biomass exclusive of the initial period of increase during the first 2 wk of the experiment (fig. 3A). *Daphnia* populations in the two enclosures with the next lowest removal rates appeared to be cycling, but the sampling window included days with both maximum and minimum densities (fig. 3B). Time-averaged *Daphnia* biomass in the latter two enclosures was slightly higher than in the enclosure with zero removal during the sampling window (fig. 2).

The effect of *Daphnia* on total phytoplankton biomass was nonlinear, with the effect being strongly negative at

Daphnia densities $< \sim 400 \mu\text{g L}^{-1}$ and weak or nonexistent at *Daphnia* densities $> \sim 400 \mu\text{g L}^{-1}$ (fig. 4). For the raw data, the shape of *Daphnia*'s effect did not fit a polynomial regression model, looking more like a threshold than a continuous function (fig. 4). To generate statistical tests of the significance of the nonlinearity, I log-transformed response variables and applied polynomial regression. These analyses showed that *Daphnia*'s effect on total phytoplankton carbon (on the basis of chlorophyll measurement) was significantly nonlinear (table 1). The same nonlinear effect was apparent when total phytoplankton biomass was calculated from microscope counts or when sestonic carbon was measured (table 1). The effect of *Daphnia* on the biomass of six of the 10 common phytoplankton species was also strongly nonlinear (figs. 5, 6; table 1). Of these six species, one (*Anabaena flos-aquae*) showed evidence of an increase in abundance at the highest *Daphnia* densities (fig. 6). For the species-specific data, the weakening of *Daphnia*'s effect also occurred at *Daphnia* densities $> \sim 400 \mu\text{g L}^{-1}$. The general conclusion that *Daphnia*'s effects were strongly nonlinear was not sensitive to the exact combination of sampling dates included in the sampling-window averages (data not shown).

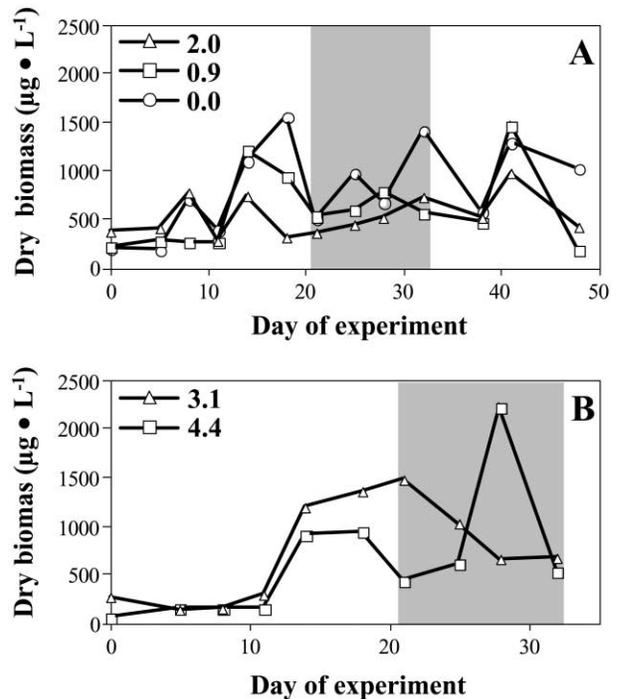


Figure 3: *Daphnia* population dynamics in the five enclosure treatments with the lowest rates of *Daphnia* removal (numbers next to symbols refer to number of removal hauls per week). Shaded areas delineate the sampling window over which the effect of *Daphnia* on phytoplankton abundance was determined.

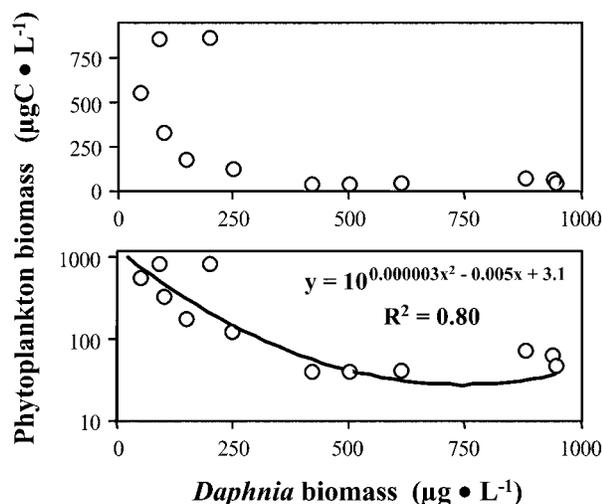


Figure 4: Effect of *Daphnia* on total phytoplankton biomass (arithmetic and logarithmic scales). All regression coefficients listed were statistically significant ($P < .05$).

The removal manipulation had a positive effect on TP (linear regression, $P < .005$) but no effect on SRP concentrations ($P > .15$). There were no significant effects of *Daphnia* on TP ($P > .10$) or SRP ($P > .60$). The SRP concentrations ranged from 180 to 240 $\mu\text{g L}^{-1}$, well above levels known to saturate algal growth (Grover 1989; Sommer 1991), in all the enclosures. Given that phosphorus was not limiting algal growth in the enclosures, it is not surprising that the C : P ratio of edible seston (1–35 μm), a potential measure of stoichiometric food quality for *Daphnia* (Sterner and Hessen 1994), was relatively low across all enclosures (range, 78–124 by atoms) and not affected by the removal gradient or by *Daphnia* ($P > .15$).

Mortality Rate Measurement

Daphnia pulex accounted for about 90% of total zooplankton biomass in the mortality rate experiment. As expected, small diatoms (*Cyclotella*, *Nitzschia*) and cryptophyte flagellates (*Cryptomonas*, *Rhodomonas*) were the most vulnerable taxa (fig. 7). In general, the most resistant taxa were chlorophytes, of which two species (*Coelastrum*, *Sphaerocystis*) were observed to form colonies up to 45 μm in diameter in the enclosure experiment. However, the most resistant species were two small, unicellular chlorophytes of the genus *Schroederia* (fig. 7).

To address the question of whether the phytoplankton assemblage shifted to dominance by less vulnerable species at high *Daphnia* densities, I calculated a vulnerability index for the assemblage as a whole on the basis of these mortality rates. Mortalities were first relativized by assigning

a value of 1 to the species (*Cryptomonas erosa*) with the highest mortality (Vanderploeg and Scavia 1979). I then calculated an overall vulnerability score for the phytoplankton community during the sampling window of the enclosure experiment by summing the products of each species' relativized mortality rate multiplied by that species' relative abundance (as a percentage of total phytoplankton biomass). The maximum value of the community vulnerability index is 100, corresponding to a monoculture of *C. erosa*, the most vulnerable species.

Although the relative mortalities of the phytoplankton species in Zaca Lake varied over two orders of magnitude (0.016–1), and the overall vulnerability of the phytoplankton community varied substantially across the large enclosures (15–49), *Daphnia* grazing did not decrease the overall vulnerability of the phytoplankton community (fig. 8A; one-tailed *F*-test, $P > .30$). *Daphnia* affected the relative abundance of three species in the enclosure experiment, and of these, the effect on *Coelastrum microporum*, a highly grazing-resistant species (fig. 7) and the overall biomass dominant, was the most pronounced (fig. 9). Despite the low vulnerability of this species, the relative abundance of *C. microporum* declined markedly as *Daphnia* biomass increased (fig. 9), which largely accounts for the lack of a decrease in community vulnerability across the *Daphnia* gradient (fig. 8A).

I also examined the data for evidence of within-species changes in morphological defense across the *Daphnia* gradient. *Coelastrum microporum* was the only species in the enclosure experiment known from previous studies to develop into larger colonies when exposed to chemical cues from dense *Daphnia* populations (van Donk et al. 1999). However, there was no evidence for an increase in colony size across the *Daphnia* gradient (fig. 8). Moreover, *Coelastrum* colony size was minimal over the part of the gradient where *Daphnia*'s effect weakened (250–600 $\mu\text{g L}^{-1}$).

Discussion

The responses of total phytoplankton biomass and most of the dominant phytoplankton species to the *Daphnia* gradient were strongly nonlinear and showed a weakening of *Daphnia*'s effect at high *Daphnia* densities (figs. 4, 5). *Daphnia* densities in the sampling window fell within the natural range of *Daphnia* densities in Zaca Lake (Sarnelle 1997) and were representative of long-term averages (fig. 3). Consequently, the decelerating effect of *Daphnia* was not a function of including transient unsustainable consumer densities in the experimental gradient. For example, phytoplankton abundance was driven to minimal levels in the zero-removal enclosure on day 21 (total phytoplankton carbon = 42 $\mu\text{g C L}^{-1}$) and remained at low levels until day 49, without any consistent downward trend in *Daph-*

Table 1: Polynomial regressions describing the effect of *Daphnia* biomass on phytoplankton response variables

Response variable	Linear		Quadratic	
	Proportion explained	P value	Proportion explained	P value
Total phytoplankton carbon ^a	.56	.002	.24	.010
Total phytoplankton biomass ^b	.48	.001	.36	.002
Particulate carbon <149 μm^c	.66	.001	.19	.008
Particulate carbon <35 μm^c	.67	.001	.19	.007
<i>Coelastrum microporum</i>	.63	.002	.19	.013
<i>Cyclotella menighiniana</i>	.83	.001	.12	.010
<i>Cryptomonas erosa</i>	.43	.000	.46	.000
<i>Rhodomonas minuta</i>	.40	.012	.25	.034
<i>Nitzschia</i> spp.	.32	.002	.41	.005
<i>Anabaena flos-aquae</i>	.00	.004	.64	.003
<i>Oocystis</i> sp.	.44	.070	.11	.182
<i>Chlamydomonas</i> spp.	.05	.999	.00	.886
<i>Schroederia setigera</i>	.24	.205	.08	.344
<i>Schroederia judayi</i>	.00	.128	.25	.118

Note: Listed are the proportion of total response variation explained by each predictor variable (linear, quadratic) and the *P* value associated with the significance of each coefficient when both predictors are in the regression model. All response variables were log transformed.

^a Based on chlorophyll.

^b Based on microscope counts.

^c Based on carbon analyzer.

nia biomass (fig. 3), indicating that the *Daphnia* in this enclosure were not slowly starving to death but rather fluctuating around an equilibrium.

The decelerating effect was also not an artifact of the method used to calculate *Daphnia* biomass from measurements of body length. I used a single length-mass equation to calculate the mass of individual *Daphnia*, and it is known that *Daphnia* condition (individual mass at length) varies with food concentration (Geller and Müller 1985); thus, it might be construed that the range of *Daphnia* biomass was inflated because animals at high density had lower condition than animals at low density. However, reduced *Daphnia* condition cannot account for the non-linear responses I report because food abundance was roughly constant across the six to seven enclosures with the highest *Daphnia* biomass (fig. 4). The *Daphnia* in these enclosures should not have varied markedly in condition, so this potential artifact cannot account for the large range of *Daphnia* biomass over which the *Daphnia* effect was nil.

The enclosure results are directly comparable to one previous study (Leibold and Tessier 1998) in which a gradient of zooplankton removal was applied over a timescale that was presumably sufficient to allow zooplankton populations to equilibrate to the manipulation (1 mo). Leibold and Tessier (1998) only reported the responses of zooplankton and algal biomass to the removal gradient, so I digitally extracted and reanalyzed their data to examine

the relationship between phytoplankton and *Daphnia* abundance as well. The direct responses of consumer abundance to consumer removal and of prey abundance to a consumer gradient should be subject to less residual error and so should be more suitable for examining subtleties of response shape than the indirect response of prey to consumer removal (where error propagates from one response to the next). Despite some notable differences between the two experiments (Leibold and Tessier worked in a low-nutrient lake and reported *Daphnia* abundance as density, not biomass, and another herbivore, the copepod *Diaptomus*, was also negatively affected by their removal manipulation), the data from their experiment are reasonably congruent with my results. Leibold and Tessier's data show suggestive visual evidence of a deceleration both in the response of *Daphnia* to the removal gradient and in the relationship between *Daphnia* density and phytoplankton biomass (fig. 10), although in each case the statistical significance of the quadratic term was marginal ($P < .065$ for the *Daphnia* response, $P < .085$ for the *Daphnia*-phytoplankton relationship). However, given the substantial increases in proportion of variation explained (when the quadratic term was included, R^2 increased from 0.61 to 0.82 for the *Daphnia* response and from 0.49 to 0.74 for the *Daphnia*-phytoplankton relationship) and the relatively low sample size ($N = 8$), there is at least suggestive evidence of decelerating responses in their experiment. In my experiment, the response of *Daphnia* biomass

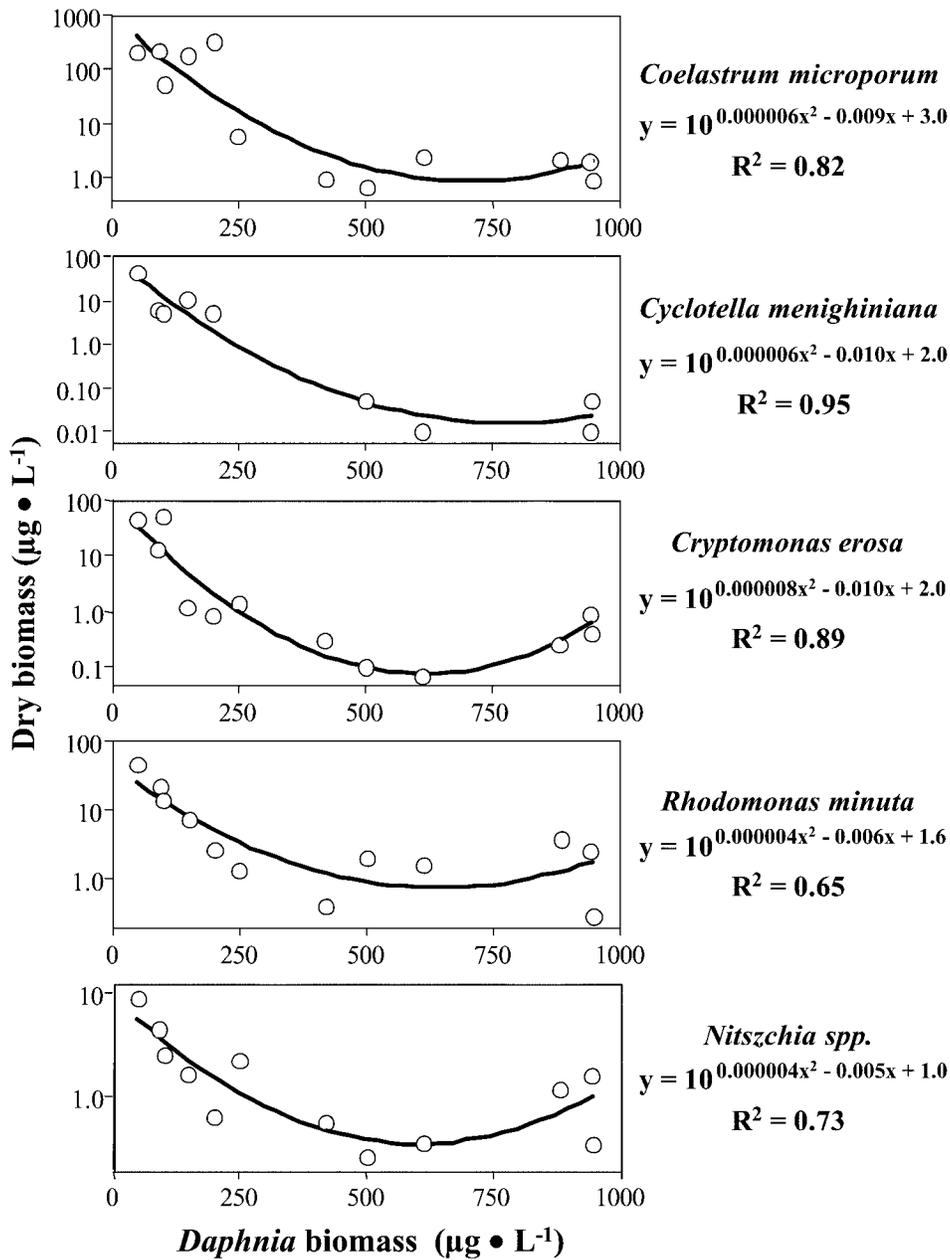


Figure 5: Effect of *Daphnia* on the abundance of common phytoplankton taxa. All regression coefficients listed were statistically significant ($P < .05$).

to the removal gradient was similarly suggestive of a decelerating response (fig. 2), but clear statistical evidence is lacking, primarily because of high values of *Daphnia* biomass in the two enclosures with cycling *Daphnia* (figs. 2, 3). Without these two enclosures, the statistical significance of the quadratic term for *Daphnia*'s response to the removal gradient was marginally significant ($P < .075$, R^2 improvement from 0.72 to 0.83).

To interpret specific experimental results in light of theoretical predictions, I analyzed in more detail the consumer-prey model with a Type III functional response. These analyses showed that there can be strong decelerating relationships between the removal gradient and *Daphnia* abundance and between *Daphnia* and phytoplankton abundance, while at the same time the indirect response of phytoplankton abundance to the removal gra-

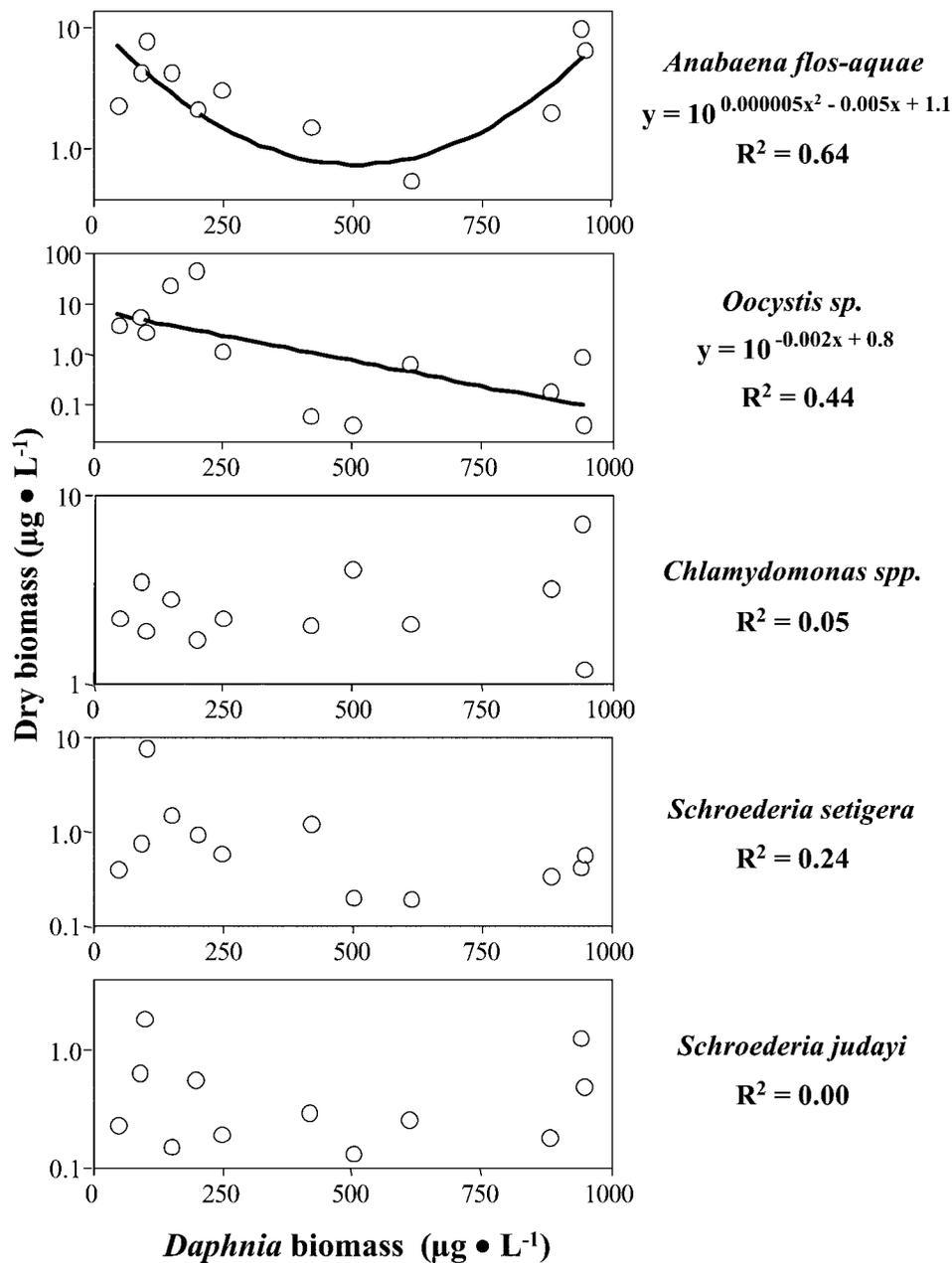


Figure 6: Effect of *Daphnia* on the abundance of common phytoplankton taxa. All regression coefficients listed were statistically significant ($P < .05$).

dient is nearly linear (fig. 11). This may explain why Leibold and Tessier's data are suggestive of nonlinear direct responses (fig. 10), yet there was a linear indirect response of phytoplankton biomass to the removal gradient (Leibold and Tessier 1998). In my experiment, there was also no evidence of nonlinearity in the indirect phytoplankton response ($P > .20$ for quadratic regression term). Taken

together, the match between theoretical predictions and the responses in these two experiments (figs. 2, 4, 5, 10) suggest that decelerating effects should be expected in *Daphnia*-phytoplankton systems.

Decelerating *Daphnia* effects contrast with linear effects seen in short-term zooplankton gradient experiments (McCauley and Kalff 1987; Elser and MacKay 1989; Elser

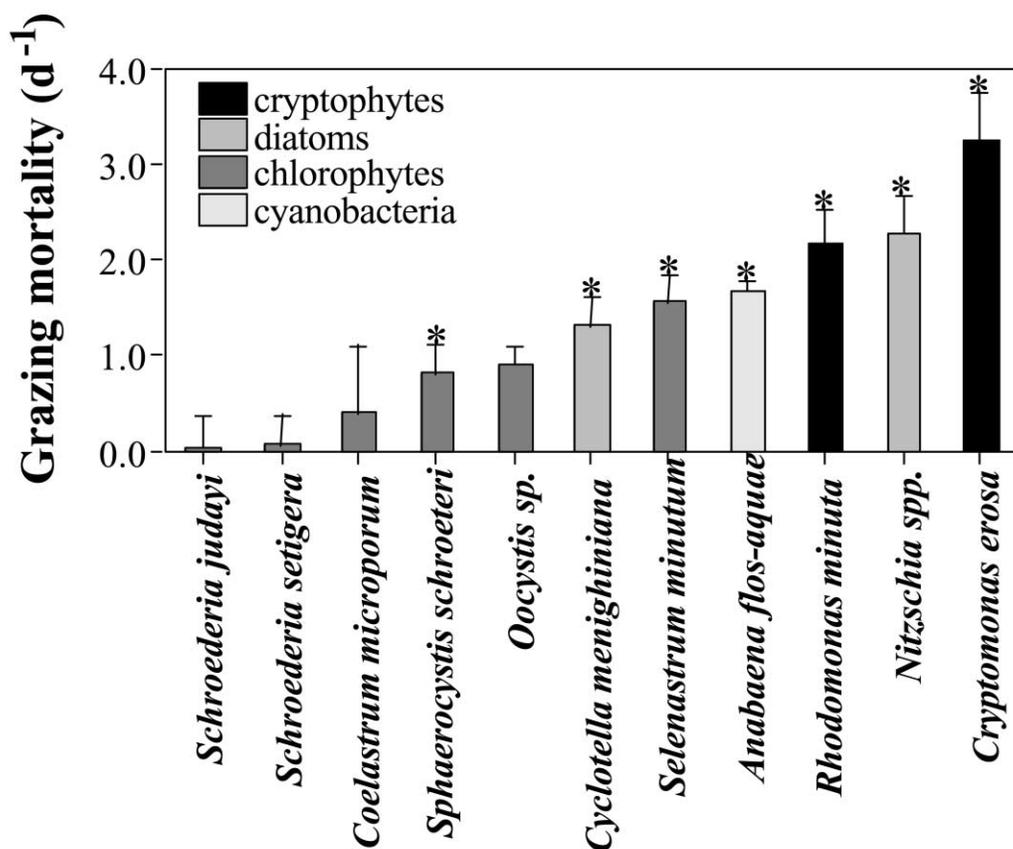


Figure 7: Results of a short-term experiment measuring species-specific phytoplankton mortalities caused by *Daphnia* grazing. Errors bars represent standard errors. Asterisks indicate that mortality rates were significantly different from 0 ($P < .05$).

et al. 1990). None of the short-term gradient studies I examined (each comprised of several experiments and/or multiple responding phytoplankton species) reported a single instance of a decelerating effect (but see Sommer et al. 2001). This contrast between linear effects in short-term experiments and the decelerating effects reported here may be a consequence of the time required for the phytoplankton to be driven to the herbivore's R^* (minimum resource requirement at equilibrium; Tilman 1982) and for the herbivore's feeding behavior to respond to chronic low food.

Mechanisms

There are at least four general mechanisms that could explain the deceleration in *Daphnia*'s effect: a shift toward resistant prey at high consumer densities, interference among consumers, a spatial refuge for the phytoplankton, or a reduction in *Daphnia*'s filtering effort at low food density (Type III functional response; Holling 1959). Of

these, a shift toward resistant prey at high consumer densities was explicitly examined via contemporaneous quantification of phytoplankton vulnerability to *Daphnia* grazing (fig. 7). These data provided no clear evidence that either the phytoplankton assemblage or the dominant species (*Coelastrum microporum*) became more resistant as *Daphnia* grazing intensity increased (fig. 8). The decelerating responses of six of the most abundant phytoplankton species provide additional evidence that consumption resistance was not primarily responsible for the weakening of *Daphnia*'s effects. It seems unreasonable to postulate that all six species responded to the *Daphnia* gradient with induced defenses against grazing, particularly in the absence of any independent evidence of such induced responses in most of these species (van Donk et al. 1999). It is also unlikely that filamentous cyanobacteria reduced *Daphnia*'s filtering rates on all species simultaneously via interference with food collection, since densities of *Anabaena flos-aquae*, the only filamentous species found in the enclosures, were very low in all treatments relative to den-

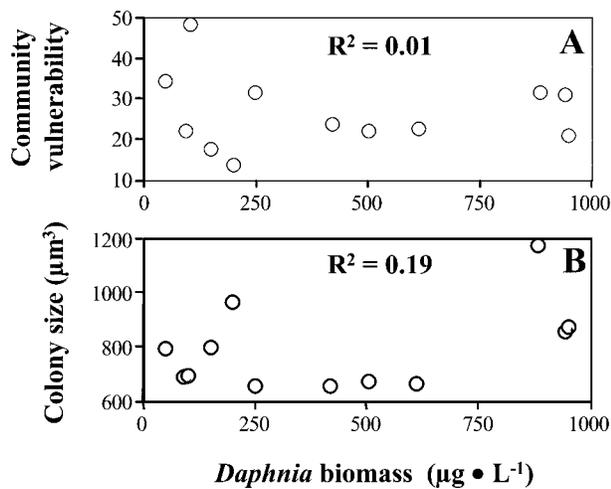


Figure 8: Effect of *Daphnia* on phytoplankton vulnerability to grazing. A, *Daphnia* biomass versus overall grazing vulnerability of the phytoplankton community. B, *Daphnia* biomass versus colony size of *Coelastrum microporum*, the most abundant phytoplankton species.

sities shown to reduce *Daphnia* filtering rates in laboratory experiments (Holm et al. 1983; Hawkins and Lampert 1989). In addition, the largely negative effect of *Daphnia* on *Anabaena* in this (fig. 6) and previous enclosure experiments in Zaca Lake (Sarnelle 1993) argues against any toxic effects of this phytoplankter on coexisting *Daphnia* (Porter and Orcutt 1980). Likewise, there was no effect of *Daphnia* on the C : P ratio of edible particles and, thus, no evidence for stoichiometric changes in phytoplankton food quality.

Two other potential explanations for *Daphnia*'s nonlinear effects, consumer interference and spatial refuge, are also unlikely to have been operating in the enclosure experiment. Intraspecific interference is known to occur in *Daphnia* but only at densities far above the highest densities found in the enclosures. For example, the lowest experimental densities employed in studies of conspecific density effects on *Daphnia* feeding (Hayward and Gallup 1976: $1,800 \mu\text{g L}^{-1}$; Helgen 1987: $3,000 \mu\text{g L}^{-1}$; Matveev 1993: $850 \mu\text{g L}^{-1}$) are near or far above the maximum densities in the enclosures (fig. 2). These studies were primarily designed to detect interference rather than to assess its importance in nature (Helgen 1987).

A spatial refuge for the phytoplankton also seems an unlikely explanation for the weakening of *Daphnia*'s effect at high densities, given that the enclosures were relatively well mixed by the removal manipulation. Dissolved oxygen profiles taken immediately before and after hauling the removal net indicated a major decrease in vertical heterogeneity caused by the manipulation technique (O. Sarnelle,

unpublished data). Under low-mixing regimes, the possibility exists for partial spatial segregation of *Daphnia* and motile phytoplankton via opposing vertical migration behavior (Jones 1988), but this refuge has never been demonstrated to affect phytoplankton mortality under natural or laboratory conditions. In the enclosure experiment, both motile and nonmotile phytoplankton showed similar decelerating responses (fig. 5), so this mechanism can be discounted.

The simplest explanation for the weakening of *Daphnia*'s effect at high *Daphnia* and low phytoplankton densities is that *Daphnia* reduces its filtering effort at low food levels. This explanation contradicts conventional wisdom about *Daphnia*'s functional response (Hallam et al. 1990; McCauley et al. 1990) and so merits closer examination. Classic laboratory studies of *Daphnia* functional response have concluded that *Daphnia* feeds with a Type I (with saturation) or Type II functional response (McMahon and Rigler 1965; DeMott 1982; Porter et al. 1982). However, the standard technique for measuring *Daphnia* feeding involves the uptake of a radioactive tracer, a technique whose precision typically declines markedly at low food levels (Porter et al. 1982), leading to low statistical power

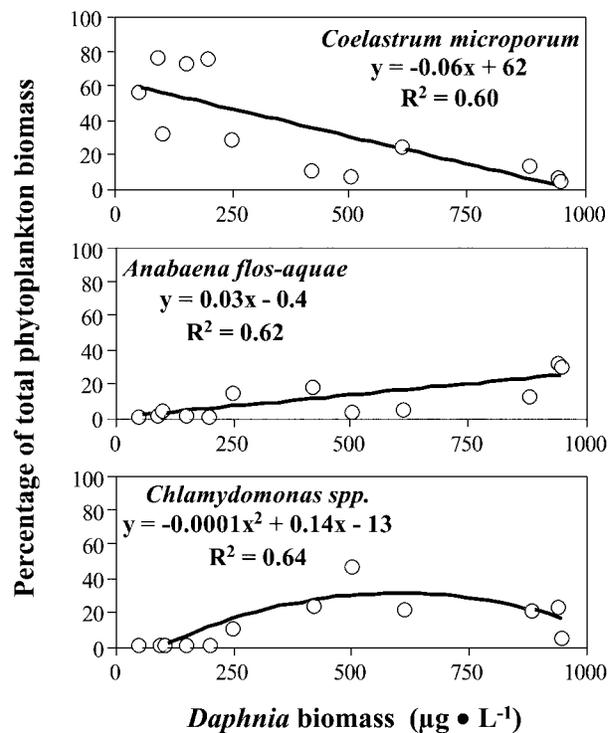


Figure 9: Effect of *Daphnia* on the relative abundance of three phytoplankton taxa. All regression coefficients listed were statistically significant ($P < .05$).

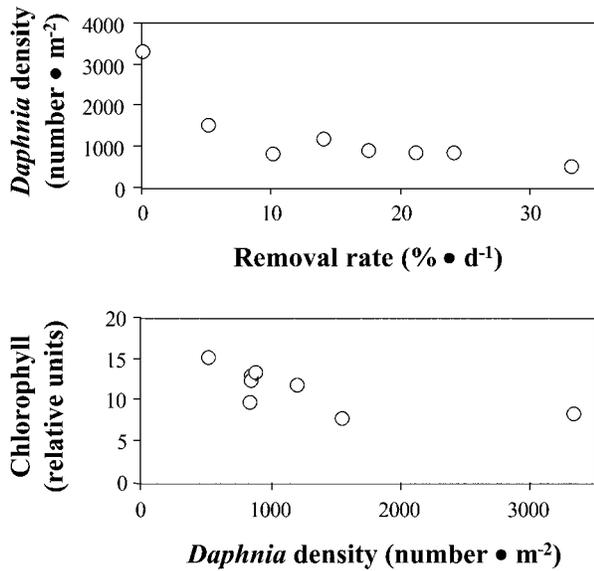


Figure 10: Effect of zooplankton removal on *Daphnia* density (top) and resulting relationship between *Daphnia* density and epilimnetic algal biomass (bottom) from Leibold and Tessier (1998).

to detect reductions in filtering effort at low food. In addition, the time allowed for animals to acclimate to food density treatments in laboratory experiments is typically very short (minutes to hours) relative to the timescale over which nonlinear effects may be expressed in nature (days to weeks). Thus, it is not clear that the design of most laboratory feeding experiments is adequate for detecting reduced filtering effort at low food. Using a targeted design, Plath (1998, 1999) recently showed that individual *Daphnia* reduce their filtering effort at low food densities, as predicted by energy optimization models (Lehman 1976). These laboratory observations are also consistent with a meta-analysis of field measurements of *Daphnia* feeding, which suggested a sharp reduction in filtering effort at low food densities (Chow-Fraser and Sprules 1992).

Plath (1998, 1999) cultured *Daphnia* at each experimental food level instead of culturing at high food and then acclimating animals to low food for a few minutes or hours, as done in previous laboratory studies. This protocol rules out transient starvation-related exhaustion as the cause of reduced activity (Muck and Lampert 1980, 1984). In Plath's study, filtering effort (as measured by the rate at which animals beat their thoracic appendages) began to decline in *Daphnia* reared at food levels below $250 \mu\text{g C L}^{-1}$, which approximates phytoplankton levels where *Daphnia*'s effect weakened in the enclosure experiment (fig. 4). Further, phytoplankton biomass at the lower asymptote in figure 4 ranged from 39 to $75 \mu\text{g C L}^{-1}$, which is similar to estimates of *Daphnia*'s R^* ($40 \mu\text{g C L}^{-1}$) when

fed the algal species employed by Plath (Kreutzer and Lampert 1999). Thus, there is considerable quantitative congruence between laboratory estimates of R^* , food levels at which *Daphnia*'s filtering effort declines, and the enclosure results.

General Implications

The evidence that *Daphnia* may feed with a Type III functional response has implications beyond planktonic or

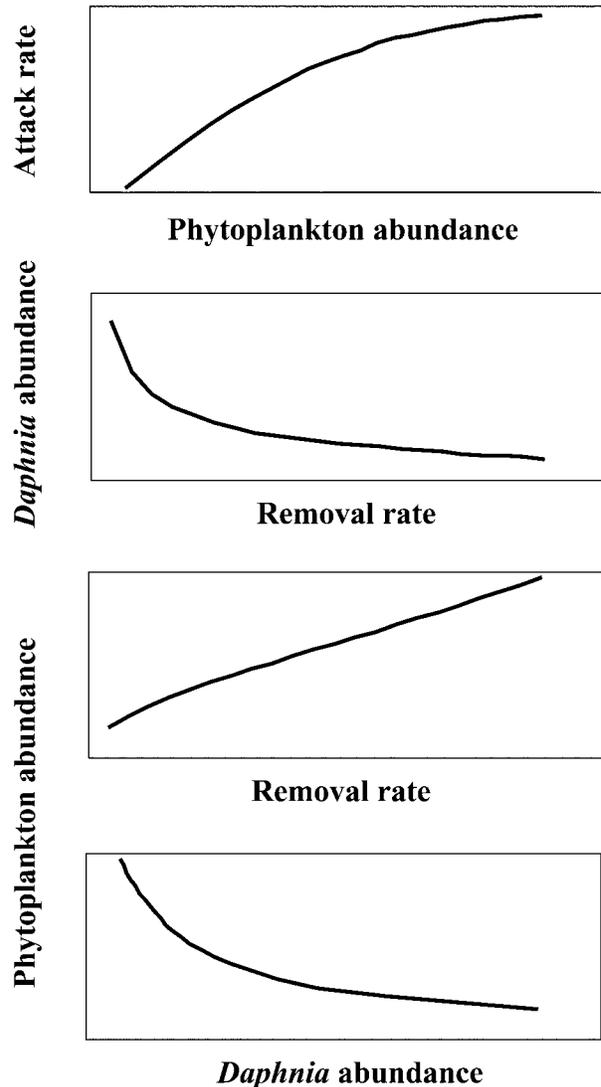


Figure 11: Theoretical predictions from a simple consumer-prey (*Daphnia*-phytoplankton) model with a Type III functional response. Consumer death rates were varied within a range where consumer attack rates increased monotonically with phytoplankton abundance (top panel). Parameter values were the same for all panels.

aquatic systems. Whether a consumer feeds with a Type II or Type III functional response is critical to the stability of the consumer-prey interaction, so the nature of the functional response is central to understanding predator-prey dynamics (Murdoch and Oaten 1975; Hassell et al. 1977). The *Daphnia*-phytoplankton system is one of the best-studied consumer-prey interactions (McCauley et al. 1990), yet a very basic assumption about *Daphnia*'s biology, that the functional response is Type I or II, may be wrong in a critical way. If *Daphnia* typically reduces its filtering rate at food densities that are well above *Daphnia*'s R^* (Chow-Fraser and Sprules 1992; Plath 1998, 1999), the evaluation of stabilizing mechanisms in *Daphnia*, a topic of general interest in ecology (McCauley and Murdoch 1987; Nisbet et al. 1991; Murdoch et al. 1998), may need to be reconsidered. More attention to *Daphnia* feeding behavior at low food levels is needed, since *Daphnia* frequently live under minimal food conditions in nature (fig. 4; Kerfoot et al. 1985; McCauley et al. 1990).

To gauge the incidence of decelerating effects in the literature, I examined 104 recent studies reporting the effect of consumers (carnivores and herbivores) on prey abundance in field experiments. I found 22 studies that employed >3 consumer density treatments, all of which were performed in aquatic systems. Seventeen of these studies reported negative effects of the consumer on prey abundance (table 2). Of these 17, 12 showed obvious visual evidence of a decelerating effect (although statistical tests for nonlinearity were typically not performed), while five studies reported effects that appeared to be linear. Interestingly, 10 of the 12 studies showing decelerating effects

examined the effects of a consumer (four carnivores, six herbivores) on benthic prey, while three of the five studies showing linear effects examined effects on pelagic prey (table 2). These trends are perhaps not surprising since benthic prey have a more obvious habitat refuge than planktonic prey, at least in experimental arenas. The conclusion that decelerating effects are common in nature must be tempered by the fact that only four of the 12 studies employed consumer densities that were clearly not above ambient densities (table 2).

Decelerating effects of consumers on prey density appear to be common, particularly in systems with benthic prey (table 2), which supports expectations based on theoretical analyses of the adaptive behavior of prey (Abrams 1993b). In benthic systems, the obvious explanation for the weakening of the consumer's effect at high consumer densities is increased per capita use of spatial refuges by prey (Diehl et al. 2000). Induced behaviors by mobile prey to the presence of predators (Peacor and Werner 1997; Anholt and Werner 1999; Diehl et al. 2000) are consistent with this explanation. Although several studies have examined the effects of a gradient of planktonic herbivores, only one previous study was of long enough duration to allow the herbivore population to approach an equilibrium (Leibold and Tessier 1998). It is perhaps not a coincidence that the latter study is the only one showing results similar to those in this article (but see Sommer et al. 2001).

My experimental results and review of recent experimental literature suggest that nonlinear consumer effects are strong and widespread (at least in aquatic systems), as suggested by Abrams (1993b, 2001). This conclusion has

Table 2: Summary of 17 published studies having >3 consumer-density treatments (including zero density) and finding negative effects on prey abundance

Study	No. of consumer treatments	Consumer	Prey	Response	Ratio of highest treatment density : ambient density
Flecker 1984	4	Carnivore	Benthic	Decelerating	?
Mittelbach 1988	6	Carnivore	Benthic	Linear	2
Posey and Hines 1991	4	Carnivore	Benthic	Linear	1
Diehl 1995	5	Carnivore	Benthic	Decelerating	4
Navarrete 1996	4	Carnivore	Benthic	Decelerating	1
Diehl et al. 2000	8	Carnivore	Benthic	Decelerating	?
Persson and Greenberg 1990	5	Carnivore	Pelagic	Decelerating	?
Hart 1987	4	Herbivore	Benthic	Decelerating	2
Hill and Knight 1987	4	Herbivore	Benthic	Decelerating	4
Lamberti et al. 1987	4	Herbivore	Benthic	Decelerating	2
Hill and Knight 1988	4	Herbivore	Benthic	Decelerating	3
McCormick and Stevenson 1989	5	Herbivore	Benthic	Decelerating	1
Feminella and Resh 1990	5	Herbivore	Benthic	Decelerating	1
Elser and MacKay 1989	6	Herbivore	Pelagic	Linear	8
Elser et al. 1990	5	Herbivore	Pelagic	Linear	8
McCauley and Kalff 1987	15	Herbivore	Pelagic	Linear	1
Leibold and Tessier 1998	8	Herbivore	Pelagic	Decelerating	1

major implications for the linkage between field manipulations of consumer abundance and models of species interactions. It has been proposed that, under certain conditions, the magnitude of a consumer's effect on prey density in a field experiment provides an estimate of the interaction coefficient in a dynamic model of the consumer-prey interaction (Osenberg et al. 1997; Laska and Wootton 1998). This proposal has been criticized primarily on the grounds that interaction strength is not likely to be a simple parameter in nature but rather a variable dependent on, among other things, the adaptive behavior of prey and indirect effects mediated by other species (Abrams 2001). The demonstration that *Daphnia's* effect on phytoplankton density was very strong from low to moderate *Daphnia* densities and essentially nil from moderate to high *Daphnia* densities (figs. 4–6) precludes any effort to parameterize an interaction model having a constant interaction coefficient. In this particular case, the mechanism underlying the deceleration in *Daphnia's* effect did not appear to be a function of any adaptive responses by the prey or indirect effects of other species but was more likely due to the simple, adaptive behavior of reduced foraging effort by the consumer at low food density. Thus, even the simplest of consumer-prey interactions should not be expected to yield reliable estimates of an interaction strength coefficient, since the latter is not likely to exist.

How then can we more directly link the results of field manipulations to ecological theory? It has been suggested that a greater emphasis on short-term experiments would be desirable in order to isolate and measure the direct effects of consumers (Bender et al. 1984; Abrams 2001), with those measurements serving as input to predictive dynamic models. This approach is predicated on the supposition that indirect effects take longer to be expressed than direct effects, an assumption that is invalid in herbivore-phytoplankton systems (Sterner 1986). Even in systems where indirect effects do not interfere with the measurement of direct effects over short timescales, it is difficult to justify the expense of field experiments for the restricted objective of measuring a consumer's attack rate. To the extent that attack rates vary with consumer or prey density, the expense of such an approach is magnified, since gradient designs would be required. Experimental field ecologists have largely ignored suggestions that they place greater emphasis on short-term responses, perhaps because of the critical need for long-term experiments in addressing applied problems (Oksanen 2001). It seems more efficient to parameterize dynamic models with less expensive natural history observations and laboratory and microcosm experiments (Abrams 2001) and to view field experiments as large-scale tests of the predictions of parameterized models. With this approach, experimental ecologists are freed to maximize the scale of field manipulations

so as to examine theoretical predictions over the long term (to better coincide with the equilibrium predictions of most models) and at the spatial scale of natural phenomena. To date, however, most large-scale field experiments have not been cast as tests of explicit models (for recent exceptions, see Schmitz 1997; Sarnelle 1999; Diehl et al. 2000).

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