

Strong and weak trophic cascades along a productivity gradient

Jonathan M. Chase

Chase, J. M. 2003. Strong and weak trophic cascades along a productivity gradient. – *Oikos* 101: 187–195.

Variation in the strengths of predator effects, although commonly observed in natural communities, and predicted from theoretical models, remains poorly understood in the study of food web interactions and community structure. In this study, I first showed that prey species in benthic pond food webs were highly variable in their susceptibility to predators. Some were vulnerable throughout their lives, whereas others were vulnerable as juveniles, but able to grow to a size-refuge. Next, I showed that herbivore and predator abundance increased along a natural productivity gradient among 29 ponds, and herbivore species composition shifted from dominance by vulnerable to dominance by invulnerable herbivore species along this gradient. However, there was a considerable amount of variation both in herbivore biomass and composition at intermediate productivity; some were dominated by small species and others by larger species. Finally, in in situ enclosure experiments, I found that predator effects were strong and cascaded to plants in a low productivity pond and in an intermediate productivity pond dominated by small herbivore species. Alternatively, in a high productivity pond and in an intermediate productivity pond dominated by larger herbivores, I found that predator effects on prey biomass were weak, and did not cascade to plants.

J. M. Chase, Dept of Biology, Box 1137, Washington Univ., Saint Louis, MO 63130, USA (jchase@biology2.wustl.edu).

Recent syntheses suggest that both resources and predators interact to structure natural food webs (Leibold et al. 1997, Persson 1999, Polis 1999, Chase 2000, Oksanen and Oksanen 2000). As a result, increased attention has been directed towards measuring the relative strengths of these factors (Brett and Goldman 1996, 1997, Osenberg and Mittelbach 1996, Wootton 1997, Laska and Wootton 1998, Berlow et al. 1999, Abrams 2001, Shurin et al. 2002). Unfortunately, the degree and consistency to which predators and resources influence prey abundance (biomass) and composition in food webs remain unclear (Leibold et al. 1997, Persson 1999, Polis 1999, Chase 2000, Chase et al. 2000a).

An important reason that many syntheses and meta-analyses have come to opposing conclusions is that these studies implicitly assume the magnitudes of these interactions are static both spatially and temporally. Most ecologists agree that food web interactions can

often be highly variable through space and time, but few studies have been explicitly designed to examine causes of this variation. Nevertheless, a variety of theoretical models are available to predict such variation. These models vary in the assumptions that they make, and in their predictions. For example, food web models vary in their assumptions of prey vulnerability, including: equal vulnerability of all prey species to predators, such that they can be lumped into a trophic level (Oksanen et al. 1981, Oksanen and Oksanen 2000); differential vulnerability to predators, such that prey species are sub-divided into vulnerable and invulnerable categories (Armstrong 1979, Leibold 1989, 1996, Abrams 1993, Holt et al. 1994); differential prey vulnerability to predators throughout their ontogeny (Chase 1999).

Each of the above assumptions about prey vulnerability to predation gives rise to a different set of predictions. Models that assume prey species are equally

Accepted 9 October 2002

Copyright © OIKOS 2003
ISSN 0030-1299

susceptible to predators predict increasing effects of predators on prey abundance along a productivity gradient (e.g., modified Lotka-Volterra food chains; Oksanen et al. 1981, Oksanen and Oksanen 2000). Alternatively, models that assume some prey vary in vulnerability to predators often predict decreasing effects of predators on prey abundance along a productivity gradient (Holt et al. 1994, Leibold 1996). This is because with increasing productivity, greater defended species become more favored, such that the relative effects of predators declines. Finally, when prey vary in their vulnerability to predators, and the species that is least dynamically affected by predators also provides better food for predators, there is potential that there are alternative stable equilibria when productivity levels are intermediate (Holt et al. 1994). Mechanisms that can lead to this case include when prey vary in their susceptibility to predators through ontogeny and are vulnerable to predators as juveniles, but invulnerable as adults (Chase 1999) and when prey are tolerant to predation, such that they are consumed, but not strongly influenced by predators (Chase et al. 2000b). In this case, predator effects are predicted to be relatively strong at low productivity, weak at high productivity, and alternative stable states, with sometimes strong, and sometimes weak predator effects at intermediate productivity (Chase 1999, Chase et al. 2000b).

In a region of small ponds in southwestern Michigan, I asked:

- (1) Are all prey species equally vulnerable to predators, or are some species more defended than others?
- (2) How do patterns of prey abundance and composition vary along a gradient of primary productivity?
- (3) Are direct and indirect predator effects consistent or variable among ponds that vary in productivity and species size-structure?

Study system

This study took place in wide variety of permanent ponds surrounding the Kellogg Biological Station (KBS, Michigan State University) in southwestern Michigan. These ponds are small, ranging from 0.5–5 ha in surface area. Primary productivity varies considerably among these ponds due to variation in nutrient inputs, light availability (influenced by the surrounding forest canopy) and turbidity (Chase 1998, Leibold 1999, Chase and Leibold 2002). Common primary producers in these ponds include periphytic diatoms, blue-green algae and filamentous green algae (primarily *Spirogyra* spp. and *Oedogonium* spp.), floating duckweeds (*Lemna minor*, *Spirodela polyrhiza*, and *Wolffia punctata*), and submerged macrophytes (primarily *Ceratophyllum demersum*, *Elodea canadensis*, *Chara vulgaris*, and several *Potamogeton* spp.). Benthic consumers (herbivore/detri-

tivores) are typically dominated by one of two species of pulmonate snails, *Physella gyrina* and *Helisoma trivolvis*. Other common herbivores (and detritivores), ranked by biomass, include amphipods (*Gammarus fasciatus* and *Hyallolella azteca*), anuran tadpoles (primarily *Rana clamitans*, *R. catesbeiana* [Ranidae], and *Hyla versicolor* [Hylidae]), other pulmonate snails (*Gyrulus parvus*, *Lymnea stagnalis*, *Pseudosuccinea collumella*), water-boatmen (Hemiptera: Corixidae), midges (Diptera: Chironomidae) and baetid mayflies (Ephemeroptera). Virtually all of these species consume a significant proportion of both plant material and detritus. Common predators (species that consume almost entirely animal material) found in most ponds include Hemipterans (*Belostoma flumineum*, *Lethocerus americana* [Belostomatidae], *Ranatra* spp. [Nepidae], Naucoridae, and Notonectidae), Odonates (*Tramea lacerata*, *Erythemis simplicicollis* [Libellulidae], *Anax junius*, *Aeshna* spp. [Aeshnidae], *Ishnura* spp., *Enallagma* spp. [Coenagrionidae], Lestidae], Dytiscid beetles (Coleoptera), and leeches (Hirudinea). Vertebrate mudminnows (*Umbra limia*), fathead minnows (*Pimephales pimelphis*), sticklebacks (*Culea constans*), adult and larval red-spotted newts (*Notophthalmus viridescens*), and tiger salamander (*Ambystoma tigrinum*) larvae also occur in several ponds.

Materials and methods

Prey vulnerability to predators in laboratory feeding trials

To examine the appropriate classification of prey species susceptibility to predators in this study system, I performed a number of feeding trials in 15 l buckets filled with well water and three 5 cm lengths of plastic macrophytes for structure. For each trial, 10 individuals of a prey species were placed together with one individual of a predator species in a bucket for 48 h, upon which time, those prey individuals remaining were considered invulnerable to that predator species. For several prey species, there was considerable size variation among individuals in nature. For these species, three size-classes were treated independently in feeding trials; small (= smallest 10%), medium (approximately the average size; middle 20%), and large (= largest 10%). Prey species used in these trials were the most common species found in the ponds and included anuran tadpoles (*Hyla versicolor*, *Rana clamitans* and *Rana catesbeiana*), pulmonate snails (*Gyrulus parvus*, *Helisoma trivolvis*, *Lymnea stagnalis*, *Physella gyrina* and *Pseudosuccinea collumella*), amphipods (*Hyallolella azteca*), chironomid midges (Diptera), and baetid mayflies (Ephemeroptera). Common predators used in these experiments were the insects, *Belostoma flumineum*, *Lethocerus americana*, *Notonecta undulatus*

(Hemiptera), *Anax junius*, *Tramea lacerta* (Odonata), leeches (Hirundae), *Dytiscus* spp. (Coleoptera), the mudminnow (*Umbra limia*), and the red-spotted newt (*Notophthalmus viridescens*). All possible predator-prey combinations were replicated three times.

Pond surveys along a natural productivity gradient

I surveyed 29 permanent ponds during August of 1997 to explore the variation in the abundance and composition of herbivore and predator trophic levels as they related to an estimated index of primary productivity. Because primary productivity in these ponds is a complex combination of light availability and nutrients, I did not indirectly estimate productivity, but instead directly estimated productivity in situ by measuring periphytic growth rates on artificial substrates in the absence of herbivory (Clesceri et al. 1998). Specifically, I suspended 0.05 m² cubical plastic tubs covered with a 0.33 mm mesh (to eliminate access by most herbivores) just below the surface of the water. Periphytic algae were allowed to grow inside this container for 15 d, after which time the algae were scraped off its inside, and analyzed for ash-free dry matter (AFDM). Three tubs were placed in each pond and averaged to account for intra-pond heterogeneity. This estimate of primary productivity correlates strongly with other standard estimates (J. M. Chase unpubl.), and provides a robust index of differences among ponds. I found that several other variables (area, depth, temperature, light, pH, conductivity, DO, TN, TP) did not explain patterns in animal abundance and composition, and I did not consider them further (Chase 1998). This does not imply that these variables are unimportant in freshwater communities, but instead reflects that I chose ponds in this survey that occurred under relatively similar

environmental conditions, aside from external nutrient inputs and light availability.

Benthic animals were sampled in five consecutive D-net (1 mm mesh) sweeps (1 m sweeps by 0.1 m net width = 0.1 m² sampled per sweep), taking care to spread sweeps across the pond to account for intra-pond heterogeneity. All benthic animals were identified and compared with taxa-specific dry-weight conversions (Chase 1998) to estimate biomass.

Experimental effects of productivity and species composition on food web interactions

To quantify the direct effects of predators on prey and the indirect of predators on the rest of the food web, I performed predator enclosure experiments in four ponds with disparate levels of productivity, as well as herbivore abundance and composition (Table 1). Specifically, one pond was chosen from the lower end of the productivity gradient, and was dominated by small-sized herbivore species (primarily the snail *Physella gyrina*, the amphipod *Hyallela azetca*, and midges). A second pond was chosen from the upper end of the productivity gradient and was dominated by large-sized herbivore species (*Helisoma trivolvis* and *Rana catesbeiana*). Finally, two intermediate productivity ponds were chosen that had nearly identical levels of productivity, but had divergent herbivore abundance and composition; one pond was dominated by small-sized herbivores, while the other was dominated by large-sized herbivores. There were no obvious differences in other chemical or physical parameters of these ponds (Table 1), and all four ponds occurred within a 0.5 km radius of each other.

In each pond, two treatments were imposed; a predator enclosure and a control. For both treatments, cages were constructed of 2.5 cm mesh vinyl-coated 'chicken

Table 1. Some properties of the four ponds used in the enclosure experiments. Animal abundances and productivity estimates were collected from the pond survey prior to the initiation of the experiment. Means plus or minus one standard deviations are given.

Variable	Pond type			
	Low	Intermediate I	Intermediate II	High
Productivity*	9.18	38.67	36.32	84.43
Area (ha)	0.14	0.17	0.11	0.22
pH	8.3	7.9	8.1	8.4
Conductivity	272	342	310	398
TN (µg/l)	987	3698	3249	4673
TP (µg/l)	32.5	165.5	188.4	434.2
Small [†] herbivore biomass (g/m ²)	2.7 ± 0.1	8.1 ± 1.1	6.3 ± 0.9	13.6 ± 1.4
Large [‡] herbivore biomass (g/m ²)	–	1.0 ± 0.6	48.4 ± 12.6	75.2 ± 18.3
Predator biomass (g/m ²)	1.2 ± 0.6	7.3 ± 1.1	17.6 ± 5.4	39.2 ± 12.3

* (mg-algae/cm²/15 days) as measured from the in situ productivity estimates (see text).

[†] Small herbivores are those species that were always vulnerable to predators, regardless of size as described in text.

[‡] Large herbivores are those species that could grow to sizes that were too large to be consumed by any of the predators as described in text.

wire' made into 0.1 m² basal area × 0.8 m tall cylinders (modified from McPeck 1998). The cages were covered with 0.03 mm mesh netting and closed at the bottom, allowing me to control access by all taxa except for algae and zooplankton, which colonized the cages freely. Each cage was embedded into the pond bottom, allowing sediments to 'seep' through the mesh, and tied down with stakes. I inoculated each cage with ambient biomass of filamentous algae and macrophytes (including floating duckweeds) that naturally occurred in each pond. All macroscopic animals were removed from these producers by hand. Periphytic algae were sampled on a 0.02 m² ceramic tile placed on the bottom of each cage. I stocked all cages with herbivores at their mean natural biomass and species composition in each pond (Table 1).

In the predator enclosure treatment, predators did not have access to the herbivores inside the cage. For the control treatments, I allowed free access by natural predators (and herbivores) by cutting four 5 × 10 cm slits into the sides of each cage near the bottom (modified after Sheldon 1987). During periodic censuses, I frequently observed a variety of predators within these cages. Thus, this treatment controls for both predator and cage effects. Each treatment was replicated with four cages. I established treatments in early June and terminated the experiment in mid-September of 1996. This time span allowed several generations of many of the numerically dominant species, and responses to treatments should represent long-term rather than transient dynamics.

At the end of the experiment, I removed macrophytes and floating algae from each cage with a small dip net, dried them at 60°C for 48 h, and weighed them. I scraped periphytic algae from each tile, and dried and weighed it as above. Periphytic and floating algae were combined into a single 'algae' category for simplicity of analyses. Non-planktonic animals were removed from each cage by pouring the contents through a 1 mm mesh sieve and into a white enamel pan. I sorted animals by taxon and trophic position (i.e. herbivore or predator), counted individuals of each group, and converted abundances into dry biomass using species and size-specific conversions (Chase 1998).

Statistical analyses

For the pond surveys, I used linear regression to analyze the relationship between the independent variable, productivity, and the dependent variables, herbivore and predator biomass, and herbivore composition (the proportion of the total biomass made up of large-invulnerable herbivores based on the results from the feeding trials).

I used ANOVA to determine if the total biomass of each trophic level varied among predator enclosure

treatments in each pond. Next, I separated producers into algae and macrophytes and herbivores into small and large size categories (size categories based on results from feeding trials). MANOVA was used to determine if the biomass of these subgroups varied among predator enclosure treatments in each pond. Following a significant MANOVA, subgroups were subsequently analyzed using univariate ANOVAs (after Bonferroni corrections). All analyses were performed using Systat 7.0 for Windows.

Results

Feeding trials

Most predators (>95%) survived throughout the feeding trial, regardless of whether they consumed any prey individuals. Results from the predation trials are shown in Table 2. All size-classes of most (8/11) of the prey taxa used in these trials were highly susceptible to predators (>90% of individuals eaten by at least one of the common predators). These vulnerable taxa included small tadpoles (*R. clamitans*, *H. versicolor*), snails (*P. gyrina*, *G. parvus* and *P. collumella*), amphipods (*H. azteca*), chironomid midges (Diptera), and baetid mayflies (Ephemeroptera). However, three common species, the snails *H. trivolvis* and *L. stagnalis* and the bullfrog tadpole, *R. catesbeiana*, were consistently invulnerable to all predator taxa when they were large. That is, while these species were vulnerable to predators when they were young (>80% of the smallest size-classes consumed by at least one predator species), they reached a size-refuge in which they were invulnerable to all predators in these ponds (0% of the largest size-classes eaten by predators, Table 2). Thus, prey in this system are best classified into two distinct groups, small-vulnerable taxa that cannot reach size-refugia and large-invulnerable taxa that can reach size-refugia.

Pond surveys along a natural productivity gradient

There was a positive relationship between primary productivity and herbivore biomass (regression; $N = 29$, $R^2 = 0.51$, $P < 0.01$; Fig. 1A), and a positive relationship between productivity and predator biomass (regression; $N = 29$, $R^2 = 0.84$, $P < 0.001$, not shown in figure). Herbivore abundance among ponds was highly variable at intermediate productivity values. I found that the residuals of the variation around this line was highest at intermediate levels of productivity using the test by Mitchell-Olds and Shaw (1987) (the peak of the relationship was significantly greater than 0 and less than 1; $P < 0.01$).

Table 2. Laboratory predator-prey feeding trial results. Values given are means, with standard deviations in parentheses.

Prey species	Percentage prey species eaten by each predator species									
	Belostoma	Lethocerous	Anax	Tramea	Dytiscus	Leech	Umbra	Notophthalmus		
Chironomid midge	69 (24)	33 (22)	100 (0)	100 (0)	100 (0)	0 (0)	100 (0)	100 (0)		
<i>Hyallala azteca</i>	100 (0)	94 (4)	100 (0)	93 (3)	74 (13)	40 (33)	82 (11)	77 (27)		
<i>Hyla versicolor</i>	88 (9)	100 (0)	100 (0)	80 (12)	0 (0)	0 (0)	22 (10)	50 (21)		
<i>Rana clamitans</i>	100 (0)	100 (0)	100 (0)	76 (9)	0 (0)	48 (23)	69 (13)	12 (5)		
<i>R. catesbeiana</i> (small ¹)	100 (0)	100 (0)	100 (0)	84 (23)	0 (0)	0 (0)	0 (0)	0 (0)		
<i>R. catesbeiana</i> (medium ¹)	36 (18)	93 (4)	76 (9)	24 (38)	0 (0)	0 (0)	0 (0)	0 (0)		
<i>R. catesbeiana</i> (large ¹)	0 (0)	5 (10)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)		
<i>Physella gyrina</i>	100 (0)	0 (0)	100 (0)	10 (9)	64 (18)	38 (21)	24 (10)	0 (0)		
<i>Gyrinus parva</i>	100 (0)	0 (0)	78 (7)	82 (16)	78 (12)	94 (8)	75 (9)	0 (0)		
<i>Pseudostaccinea collumella</i>	100 (0)	0 (0)	53 (43)	21 (12)	54 (14)	43 (24)	14 (21)	0 (0)		
<i>Heliosma trivolis</i> (small ²)	100 (0)	0 (0)	23 (34)	0 (0)	78 (14)	56 (12)	12 (11)	0 (0)		
<i>Heliosma trivolis</i> (medium ²)	66 (16)	0 (0)	0 (0)	0 (0)	57 (24)	24 (20)	0 (0)	0 (0)		
<i>Heliosma trivolis</i> (large ²)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)		
<i>Lymnea stagnalis</i> (small ³)	100 (0)	0 (0)	34 (13)	0 (0)	86 (16)	36 (25)	12 (18)	0 (0)		
<i>Lymnea stagnalis</i> (medium ³)	88 (18)	0 (0)	12 (24)	0 (0)	34 (28)	12 (21)	0 (0)	0 (0)		
<i>Lymnea stagnalis</i> (large ³)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)		

¹ Small *R. catesbeiana* = 4–8 mm, Medium = 15–20 mm, Large = 30–35 mm.

² Small *H. trivolis* = 3–5 mm, Medium = 8–12 mm, Large = 15–20 mm.

³ Small *L. stagnalis* = 2–4 mm, Medium = 6–10 mm, Large = 18–22 mm.

The proportion of large-invulnerable herbivore species (the two snails, *Heliosma trivolis* and *Lymnea stagnalis* and the bullfrog tadpole, *Rana catesbeiana*) also significantly increased with primary productivity (regression; $N = 29$, $R^2 = 0.37$, $P > 0.01$) (Fig. 1B). Again, the greatest variation around this relationship was at intermediate productivity using the Mitchell-Olds and Shaw test.

Experimental effects of productivity and species composition on food web interactions

In the low productivity pond, total herbivore biomass was nearly two-fold higher in the predator exclusion treatment relative to the control treatment (Table 3, Fig. 2A). There were no large-invulnerable herbivore species in this pond, and thus these changes in biomass were entirely due to changes in the biomass of small-vulnerable herbivores. At the producer trophic level total biomass was lower in the predator exclusion treatment relative to the control treatment; a pattern consistent with a trophic cascade (Table 3, Fig. 2B). The biomass of both subgroups of producers was significantly affected by the exclusion treatment (MANOVA; $F_{2,5} = 144.10$, $P < 0.001$). Specifically, the biomass of algae was lower in the exclusion relative to the control treatment, while the opposite was true for macrophytes (Table 3, Fig. 2B).

In the first intermediate productivity pond, which was dominated by a relatively low biomass of small-vulnerable herbivore species, total herbivore biomass was higher in the predator exclusion treatment relative to the control treatment (Table 3, Fig. 2C). Here, when examined by size categories, the overall response of herbivores to predator exclusion was significant (MANOVA; $F_{2,5} = 4354.49$, $P < 0.0001$), but this result was driven by a reduction in small-vulnerable species, since large-invulnerable species, which were rare, were unaffected (Table 3). At the producer trophic level, total biomass was lower in the predator exclusion treatment relative to the control treatment (Table 3, Fig. 2D). The biomass of both subgroups of producers was affected by the exclusion treatment (MANOVA; $F_{2,5} = 40.97$, $P < 0.001$). Specifically, the biomass of algae was lower in the exclusion relative to the control treatment, while the opposite was true for macrophytes (Table 3, Fig. 2D).

In the second intermediate productivity pond, which was dominated by large-invulnerable herbivore species (and their vulnerable juveniles), total herbivore biomass was unaffected by predators. Predators significantly altered herbivore composition (MANOVA $F_{2,5} = 36.1$, $P < 0.001$). Small-vulnerable herbivores were more abundant in the predator exclusion treatment, whereas large-invulnerable species were more abundant in the control treatment (Table 3, Fig. 2E). There was no

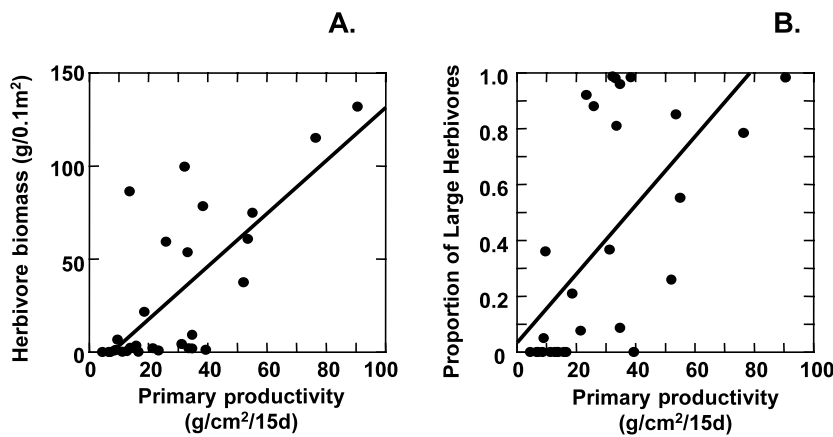


Fig. 1. (A). The relationship between herbivore biomass and estimated primary productivity from the regional survey of 29 ponds. (B) The relationship between the proportions of herbivore biomass supplied by large herbivore species and estimated primary productivity from the regional survey of 29 ponds presented in A. Note the high variation observed at intermediate productivity values in both cases.

effect of predator treatment on total producer biomass, or either sub-group of producers (MANOVA; $F_{2,5} = 0.29$, $P = 0.76$, i.e. there was not a trophic cascade; Table 3, Fig. 2F).

In the high productivity pond, total herbivore biomass was unaffected by the treatment. Predators significantly altered herbivore composition (MANOVA; $F_{2,5} = 43.74$, $P < 0.001$). Small-vulnerable herbivores were more abundant in the predator enclosure treatment, whereas large-invulnerable species were more abundant in the control treatment (Table 3, Fig. 2G). There was no effect of predator treatment on total producer biomass, or either subgroup of producers (MANOVA; $F_{2,5} = 1.27$, $P < 0.36$) (Table 3, Fig. 2H).

Discussion

In this study, I showed that there was a considerable amount of variation in the susceptibility of prey to predator species, in prey and predator biomass along a gradient of productivity in natural ponds, and in the strengths of ecological interactions along that gradient.

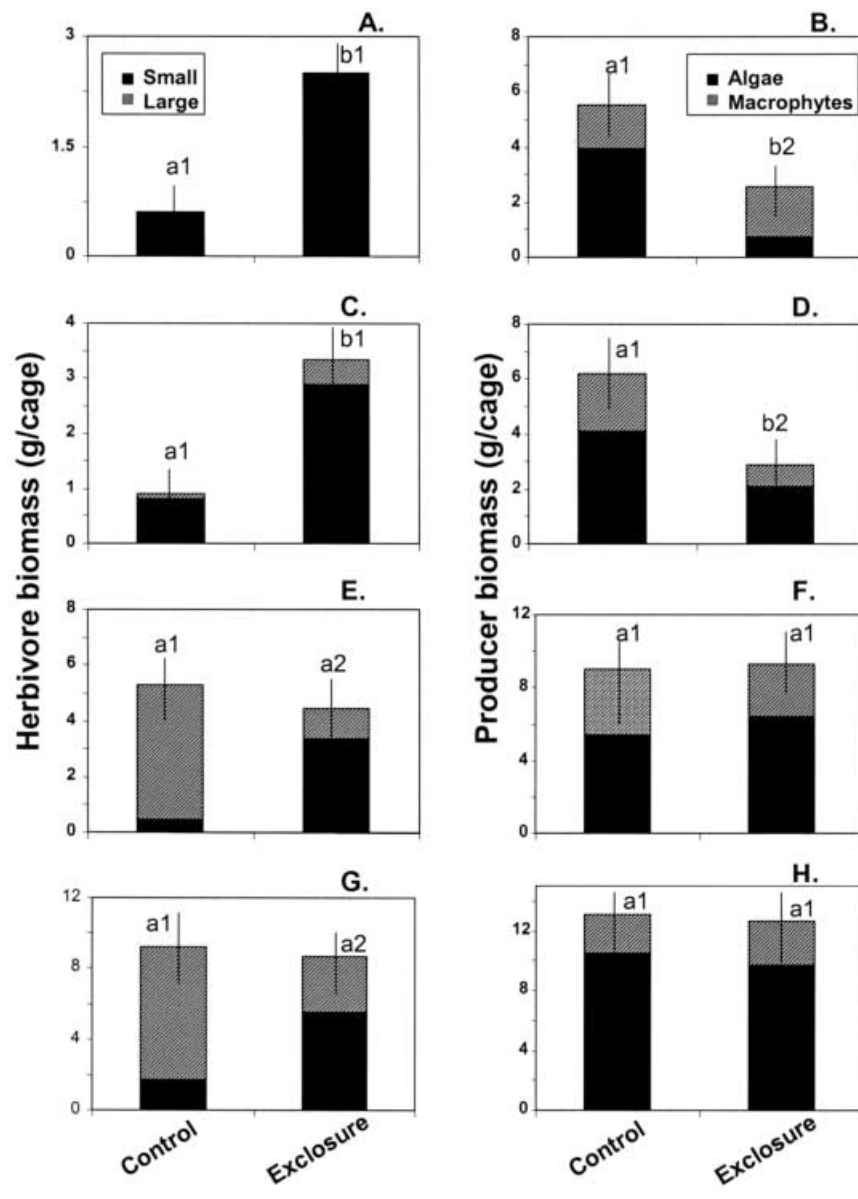
While most herbivore species were small, and susceptible to at least one of the common predator types used in the feeding trials, two snails (*Helisoma trivolvis* and *Lymnea stagnalis*) and the bullfrog (*Rana catesbeiana*), were too large to be eaten by any predators in their largest size-classes. In this system, defense against most predators seemed to result from size, rather than other

Table 3. Univariate ANOVA results from the “effects of predators” experiment. Separate analyses were performed on total herbivore and plant biomass, and on the types of herbivores (small and large) and plants (algae and macrophytes).

Response variable	df	MS	F	P
Low productivity pond				
Total herbivore biomass*	1,6	0.029	23.510	0.003
Total producer biomass	1,6	118.96	1125.95	0.0001
Algae biomass	1,6	49.51	854.69	0.0001
Macrophyte biomass	1,6	14.88	769.43	0.0001
Intermediate productivity pond I.				
Total herbivore biomass	1,6	1.96	1601.91	0.0001
Small herbivore biomass	1,6	1.11	132.21	0.0001
Large herbivore biomass	1,6	0.007	2.49	0.18
Total producer biomass	1,6	242.00	910.35	0.0001
Algae biomass	1,6	50.02	320.86	0.0001
Macrophyte biomass	1,6	72.13	385.71	0.0001
Intermediate productivity pond II.				
Total herbivore biomass	1,6	0.04	0.36	0.57
Small herbivore biomass	1,6	1.75	56.37	0.0001
Large herbivore biomass	1,6	1.26	19.04	0.005
Total producer biomass	1,6	0.332	0.70	0.43
Algae biomass	1,6	0.03	0.16	0.71
Macrophyte biomass	1,6	1.72	0.47	0.52
High productivity pond				
Total herbivore biomass	1,6	0.12	1.52	0.26
Small herbivore biomass	1,6	2.35	100.55	0.0001
Large herbivore biomass	1,6	1.42	19.31	0.005
Total producer biomass	1,6	6.72	2.98	0.14
Algae biomass	1,6	0.29	2.27	0.18
Macrophyte biomass	1,6	4.22	2.63	0.16

* No large herbivores were present in this pond.

Fig. 2. Results from the field experiment that manipulated the presence or absence of predators. A and B represent herbivore and producer responses, respectively in the low productivity pond. C and D are for the intermediate productivity pond dominated by small-vulnerable herbivores. E and F are for the intermediate productivity pond dominated by large-invulnerable herbivores. G and H are for the high productivity pond. In each set of figures, the herbivores are divided into small and large herbivore species (see text) and producers are divided into algae and macrophytes (including duckweeds). Error bars are ± 1 SD of the total biomass of each trophic level. Different letters denote significant differences on overall biomass of producer and animals between treatments (Tukey's hsd $P < 0.05$), whereas different numbers represent significant differences in the composition of a given trophic level (i.e. large vs small herbivores or algae vs macrophytes) (Tukey's hsd $P < 0.05$) (Table 3).



morphological, behavioral, or chemical defenses. The prey species, which were 'inedible', were actually susceptible to at least some predators when they were young and small. Thus, the patterns of prey susceptibility to predators does not fit the assumptions of simple food chain models, which make no distinctions among prey susceptibility to predators (Oksanen et al. 1981, Oksanen and Oksanen 2000), or food web models that assume variation in prey species susceptibility to predators throughout a prey's lifetime (Holt et al. 1994, Leibold 1996). The results are consistent, however, with the model assumptions of Chase (1999), where prey are assumed to be susceptible to predators when young but then grow to a size-refuge.

The results from the regional survey showed significant increases in both herbivore and predator biomass along the productivity gradient. Further, with increasing productivity, herbivore species composition shifted from small-vulnerable to large-invulnerable species. Both of these results are inconsistent with predictions from food chain models (Oksanen et al. 1981, Oksanen and Oksanen 2000), but consistent with predictions from food web models with and without size-structure (Holt et al. 1994, Leibold 1996, Chase 1999). I also found high variation at intermediate levels of primary productivity in both the relationship between herbivore biomass and herbivore composition. Specifically, at intermediate productivity, some ponds had a low biomass

of herbivores dominated by small species, whereas others had a high biomass of herbivores dominated by large species. This result is most consistent with the predictions of the models that assume that prey that are least affected by predators also provide better food for predators, such as the size-structured model of Chase (1999) or the prey tolerance model of Chase et al. (2000b, see also Holt et al. 1994).

Finally, I performed an in situ field experiment to examine the strengths of food web interactions in four of those ponds that varied orthogonally in productivity and species composition. I found that predator removal had strong effects on herbivores that cascaded through the food web to plants in the low productivity pond, as well as in the intermediate productivity pond that was dominated by small-vulnerable herbivore species. Alternatively, predator removal had weak effects that did not cascade to producers in the high productivity pond and the second intermediate productivity pond that was dominated by large-invulnerable herbivore species. The strength of the trophic cascade was not related to the absolute density of predators. The high productivity pond had considerably higher predator biomass ($39.2 \pm 12.3 \text{ g/m}^2$) than the low productivity pond ($1.2 \pm 0.6 \text{ g/m}^2$). Instead, the result most likely occurred because in the low productivity pond, herbivores lacked sufficient resources to grow to size-refugia, and this pond was dominated by small-vulnerable prey species. The high productivity pond, however, was dominated by herbivore species that could achieve size-refugia, and weaken the overall strength of the trophic cascade (Chase 1999). In each case where predator removal allowed herbivores to increase, not only did they decrease the overall biomass of producer species, but they also shifted the relative abundance of the two groups of producers (algae and macrophytes). This result is consistent with a variety of previous studies which showed that high herbivory altered the competitive relationships among algal species that are relatively vulnerable to herbivory, and macrophytes, which are rarely eaten (Brönmark et al. 1992, 1997).

The opposing results from the two intermediate productivity ponds occurred despite the fact that these two intermediate productivity ponds, were extremely close in proximity ($< 100 \text{ m}$ apart), and had similar physical and chemical features (Table 1). Thus, it is possible that these two ponds resided in alternative stable states, as predicted by some models (Holt et al. 1994, Chase 1999, Chase et al. 2000b). However, this possibility requires much further investigation, and a larger sampling of ponds at all levels of productivity.

Trophic cascades have been observed in a wide-variety of ecosystems (Pace et al. 1999, Chase 2000). Indeed, across studies, trophic cascades seem to be particularly strong in the benthos of freshwater ecosystems, relative to other ecosystem types (Shurin et al. 2002). However, as emphasized here, I found that even

within seemingly similar ecosystems, such as these small ponds, the strengths of trophic cascades can be highly variable; in this case likely as a result of variation in productivity and prey size-structure. Several previous studies have emphasized the role of size-refugia as a defense against predators, weakening both direct and indirect food web interactions under some conditions (Hambright et al. 1991, Hambright 1994, Persson et al. 1996). Indeed, some of the most dramatic cases of trophic cascades occur in systems in which prey are much smaller than their predators, and cannot achieve size-refugia (Estes and Palmisano 1974, Power 1990, Spiller and Schoener 1990, Carpenter et al. 2001). Finally, as with my study, size-refugia have been implicated as a mechanism leading to alternative stable states in a variety natural ecosystems (Paine 1976, Paine et al. 1985, Bazely and Jeffries 1986, Dublin et al. 1990). As such, I conclude that although across ecosystem comparisons do show differences in the strengths of trophic cascades among ecosystem types (Shurin et al. 2002), within ecosystem variation, caused by a variety of common factors, such as productivity and/or prey size-structure, can be at least as great.

Acknowledgements – This paper benefited due to discussions and comments from J. Brown, A. Downing, T. Knight, M. Leibold, M. McPeck, B. Peckarsky, C. Pfister, E. Simms, O. Schmitz, J. Shurin, T. Wootton and several anonymous reviewers. Support was provided from the Hinds Fund, NSF DEB 95-09004 (M. Leibold), and NSF DEB 97-01120 (J. M. C). Logistical support was generously provided by the Kellogg Biological Station. This is K.B.S. contribution 984.

References

- Abrams, P. A. 1993. Effect of increased productivity on the abundance of trophic levels. – *Am. Nat.* 141: 351–371.
- Abrams, P. A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. – *Oikos* 94: 209–218.
- Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. – *Ecology* 60: 76–84.
- Bazely, D. R. and Jeffries, R. L. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. – *J. Ecol.* 74: 693–706.
- Berlow, E. L., Navarette, S. A., Briggs, C. J. et al. 1999. Quantifying variation in the strengths of species interactions. – *Ecology* 80: 2206–2224.
- Brett, M. T. and Goldman, C. R. 1996. A meta-analysis of the freshwater trophic cascade. – *Proc. Nat. Acad. Sci.* 93: 7723–7726.
- Brett, M. T. and Goldman, C. R. 1997. Consumer versus resource control in freshwater pelagic food webs. – *Science* 275: 384–386.
- Brönmark, C., Klosiewski, S. P. and Stein, R. A. 1992. Indirect effects of predation in a freshwater, benthic food chain. – *Ecology* 73: 1662–1674.
- Brönmark, C., Dahl, J. and Greenburg, L. 1997. Complex trophic interactions in benthic food chains. – In: Streit, B., Städler, T. and Lively, C. M. (eds), *Ecology and evolution of freshwater animals*. Birkhäuser Publishers.
- Carpenter, S. R., Cole, J. J., Hodgson, J. R. et al. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. – *Ecol. Monogr.* 71: 163–186.

- Chase, J. M. 1998. Size-structured interactions and multiple domains of attraction in pond food webs. Ph.D. thesis, Univ. of Chicago.
- Chase, J. M. 1999. Food web effects of prey size refugia: variable interactions and alternative stable equilibria. – *Am. Nat.* 154: 559–570.
- Chase, J. M. 2000. Are there real differences among aquatic and terrestrial food webs? – *Trends Ecol. Evol.* 15: 408–412.
- Chase, J. M. and Leibold, M. A. 2002. Spatial scale dictates the productivity-diversity relationship. – *Nature* 416: 427–430.
- Chase, J. M., Leibold, M. A., Downing, A. L. and Shurin, J. B. 2000a. The effects of productivity, herbivory, and plant compositional turnover in grassland food webs. – *Ecology* 81: 2485–2497.
- Chase, J. M., Leibold, M. A. and Simms, E. L. 2000b. Plant tolerance and resistance in food webs: community-level predictions and evolutionary implications. – *Evol. Ecol.* 14: 289–314.
- Clesceri, L. S., Greeberg, A. E. and Eaton, A. D. (eds). 1998. Standard methods for the examination of water and wastewater. 20th ed. – Am. Public Health Ass.
- Dublin, H. T., Sinclair, A. R. E. and McGlade, J. 1990. Elephants and fire as cause of multiple stable states in the Serengeti-Mara woodlands. – *J. Anim. Ecol.* 59: 1147–1164.
- Estes, J. A. and Palmisano, J. F. 1974. Sea otters: their role in structuring benthic nearshore communities. – *Science* 185: 1058–1060.
- Hambright, K. D. 1994. Morphological constraints in the piscivore-planktivore interaction: implications for the trophic cascade hypothesis. – *Limnol. Oceanogr.* 39: 897–912.
- Hambright, K. D., Drenner, R. W., McComas, S. R. and Hairston Jr., N. J. 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. – *Hydrobiologia* 121: 389–404.
- Holt, R. D., Grover, J. D. and Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. – *Am. Nat.* 144: 741–777.
- Laska, M. S. and Wootton, J. T. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. – *Ecology* 79: 461–476.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. – *Am. Nat.* 134: 922–949.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. – *Am. Nat.* 147: 784–812.
- Leibold, M. A. 1999. Biodiversity and nutrient enrichment in pond communities. – *Evol. Ecol. Res.* 1: 73–95.
- Leibold, M. A., Chase, J. M., Shurin, J. B. and Downing, A. L. 1997. Species turnover and the regulation of trophic structure. – *Annu. Rev. Ecol. Syst.* 28: 467–494.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. – *Ecol. Monogr.* 68: 1–23.
- Mitchell-Olds, T. and Shaw, R. G. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. – *Evolution* 41: 1149–1161.
- Oksanen, L. and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. – *Am. Nat.* 155: 703–723.
- Oksanen, L., Fretwell, S. D., Arrüda, J. and Niemela, P. 1981. Exploitation ecosystems along gradients of primary productivity. – *Am. Nat.* 118: 240–261.
- Osenberg, C. and Mittelbach, G. G. 1996. The limitation of trophic levels. – In: Polis, G. A. and Winnemiller, K. (eds), *Food webs: integration of patterns and dynamics*. Chapman and Hall.
- Pace, M. L., Cole, J. J., Carpenter, S. R. and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. – *Trends Ecol. Evol.* 14: 483–488.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. – *Ecology* 57: 858–873.
- Paine, R. T., Castillo, J. C. and Cancino, J. 1985. Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand and Washington State. – *Am. Nat.* 125: 679–691.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. – *Oikos* 85: 385–397.
- Persson, L., Andersson, J., Wahlström, E. and Eklöv, P. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. – *Ecology* 77: 900–911.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. – *Oikos* 86: 3–15.
- Power, M. E. 1990. Effects of fish in river food webs. – *Science* 250: 811–814.
- Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. – *Ecology* 68: 1920–1931.
- Shurin, J. B., Borer, E. T., Seabloom, E. W. et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. – *Ecology Letters* 5: 785–791.
- Spiller, D. A. and Schoener, T. W. 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. – *Nature* 347: 469–472.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. – *Ecol. Monogr.* 67: 45–64.