

REPORT

A cross-ecosystem comparison of the strength of trophic cascades

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Abstract

Although trophic cascades (indirect effects of predators on plants via herbivores) occur in a wide variety of food webs, the magnitudes of their effects are often quite variable. We compared the responses of herbivore and plant communities to predator manipulations in 102 field experiments in six different ecosystems: lentic (lake and pond), marine, and stream benthos, lentic and marine plankton, and terrestrial (grasslands and agricultural fields). Predator effects varied considerably among systems and were strongest in lentic and marine benthos and weakest in marine plankton and terrestrial food webs. Predator effects on herbivores were generally larger and more variable than on plants, suggesting that cascades often become attenuated at the plant–herbivore interface. Top-down control of plant biomass was stronger in water than on land; however, the differences among the five aquatic food webs were as great as those between wet and dry systems.

Keywords

Cross-system comparison, indirect effects, meta-analysis, predation, top-down control, trophic structure.

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INTRODUCTION

Hairston *et al.* (1960) touched off 40 years of debate when they proposed that predators maintain global plant biomass at high levels by limiting the densities of herbivores (the ‘green world’ hypothesis). Trophic cascades have since been described in a wide variety of systems including lakes, streams, forests, grasslands, kelp beds, and marine plankton (Power 1990; Carpenter & Kitchell 1993; McClaren & Peterson 1994; Brett & Goldman 1996; Estes *et al.* 1998; Micheli 1999; Pace *et al.* 1999; Post *et al.* 1999; Schmitz *et al.* 2000; Halaj & Wise 2001). Because the most compelling examples of cascades come from aquatic systems, several authors have proposed that cascades are more prevalent in water than on land (Strong 1992; Polis 1999; Halaj & Wise 2001). Two recent meta-analyses of terrestrial trophic cascade experiments came to contrasting conclusions about whether trophic cascades are stronger in aquatic than in terrestrial systems (Schmitz *et al.* 2000; Halaj & Wise 2001). Differences among food webs in the strength of top-down control may have profound effects on the distribution of producer and consumer biomass among the earth’s ecosystems. The effects of human food web alterations, for instance predator extirpation through fishing or hunting, on

lower trophic levels may also vary among ecosystem types. Debate continues as to whether systematic differences in plant defences and nutritional value, body size, species diversity, productivity, or other factors lead to variation in the importance of top-down control (Strong 1992; Hairston & Hairston 1993; Polis & Strong 1996; Brett & Muller-Navarra 1997; Polis 1999; Chase 2000; Oksanen & Oksanen 2000; J.B. Shurin & E.W. Seabloom unpublished manuscript).

Several meta-analyses of trophic cascade experiments have been performed in individual systems (Brett & Goldman 1996; Micheli 1999; Schmitz *et al.* 2000; Halaj & Wise 2001); however, none has quantitatively assessed the strength of cascades across different ecosystems. We compared the effects of predator manipulations on herbivore and plant biomass among six ecosystems: lentic (lake and pond) plankton and benthos, stream benthos, marine plankton and benthos, and terrestrial systems dominated by herbaceous plants (grasses and forbs). We compiled data from 102 field experiments that measured the effects of predators on the biomass of primary producers and either the biomass or abundance of herbivores (Table 1). We estimated the effects of predators as the log ratio $\{\ln(N_{p+}/N_p)\}$ of plant and herbivore

Table 1 The number of experiments in each system, plus the number that used vertebrate or invertebrate predators.

System	<i>n</i>	Vertebrate predators	Invertebrate predators
Lentic benthos	12	6	6
Marine benthos	8	6	2
Stream benthos	33	29 (5 with both)	9 (5 with both)
Lentic plankton	22	20	2
Marine plankton	9	7	2
Terrestrial	18	3	15

densities in the presence (N_{p+}) and absence (N_p) of predators (Osenberg *et al.* 1997; Hedges *et al.* 1999). Because the 'green world' hypothesis deals specifically with the biomass of plant assemblages, not individual species (Polis *et al.* 2000), we included only studies that reported results in terms of community biomass (e.g. not measures of leaf damage, individual species responses, seed production, etc.). Our goal was to quantitatively compare the strength of cascades *among* systems using the biomass of plants and either the biomass or density of herbivores as the units of measure.

METHODS

We searched the literature for field experiments that manipulated predators and reported the responses of plant community biomass and either biomass (e.g. g/m^2) or density (e.g. $number/m^2$) of herbivores (Table 1). A list of the studies used is in Supporting Information. When results were reported as time series, we used only the final sampling date in our analysis. This was done in order to make studies with multiple sampling dates most consistent with those that presented only a single sample. For studies where predator manipulations were crossed with other treatments (e.g. nutrients), we only contrasted the predator treatments and controls under ambient conditions (e.g. in the absence of other manipulated factors). When multiple predator densities were used, we contrasted the predator-free control with the treatment that represented ambient predator density for the system. If we were unable to determine which predator treatment was closest to natural levels, we used the treatment with the lowest predator density. Percentage plant cover was used as a surrogate measure of plant biomass in some marine benthic and terrestrial studies. Primary producers in lentic and streams benthos consisted of microalgae (periphyton), whereas those in marine benthos were macro-algae in hard bottom habitats (mostly kelp forests). Five of the marine benthic studies, and one of the lentic benthic studies, were 'natural experiments' where the observers did not manipulate the predators directly.

However, predator effect sizes were very similar between natural and planned experiments.

The effect size of predator manipulations was measured as the log ratio of plant and herbivore density in the presence and absence of predators (Osenberg *et al.* 1997; Gurevitch & Hedges 1999; Hedges *et al.* 1999). We used the log ratio because it has clear biological meaning (e.g. the proportional change in the response variable). It also has good statistical properties in that it shows the least bias of several metrics, and its sampling distribution is approximately normal (Hedges *et al.* 1999). Differences among systems were tested by planned orthogonal contrasts. Although the confidence associated with the log ratios varied among studies, we did not weight the values by their precision. This was because eight of the studies were unreplicated, and several others did not report estimates of variability. Eliminating studies without variance estimates would have reduced our sample size and possibly introduced biases into our data set (Englund *et al.* 1999). Using unweighted estimates of the log ratio weakens the power to detect differences among systems (increased Type II error rate), but does not bias our estimate of the effect size (Gurevitch & Hedges 1999; Hedges *et al.* 1999). Osenberg *et al.* (1999) recommended scaling the log ratio to the duration of the experiment to incorporate time scale when the response variable changes over time. This approach is valid for studies within a system type. However because the generations times of the organisms varied greatly across systems, it is not appropriate for cross-system comparisons such as ours. In addition, examination of time series of response data for those studies that reported multiple sampling dates indicated that most studies approached approximately steady state conditions over the course of the experiments (see also Schmitz *et al.* 2000).

RESULTS

Predators reduced herbivore abundance in every system (i.e. the mean herbivore log ratio was always significantly less than zero, Fig. 1). The herbivore response was greatest in lentic and marine benthos and weakest in streams and terrestrial systems (Fig. 1). Predator effects ranged from a mean 17.3-fold reduction of herbivore density in lentic benthos (i.e. herbivore density was 17.3 times greater in the absence of predators than in their presence) to a 1.4-fold reduction in streams. Terrestrial food webs showed 1.6 times lower herbivore density with predators than without.

Plant biomass often increased in the presence of predators; however, the magnitudes of the effects were generally smaller than those on herbivores (Fig. 1). The plant effect size ranged from a 4.7-fold increase in marine benthos to a (nonsignificant) 1.1-fold increase in terrestrial systems. The plant response was significantly greater than

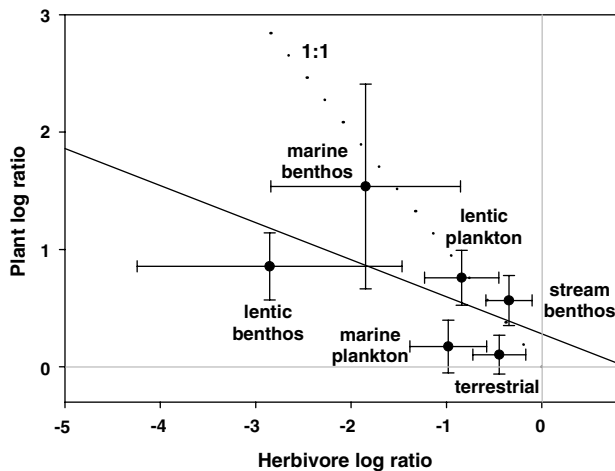


Figure 1 The effect size of predators (\log_e ratio) on primary producers vs. herbivores in six ecosystems. Error bars are 95% confidence intervals. The effect of predators is significant if the confidence interval does not overlap zero (the grey lines). There were significant differences among systems in both plant and herbivore responses (plants: one-way ANOVA, $F = 7.70$, d.f. = 5, $P < 0.0001$, $R^2 = 0.29$; herbivores: $F = 10.34$, d.f. = 5, $P < 0.0001$, $R^2 = 0.35$). The equation for the linear regression relating the plant and herbivore effect sizes (the solid line) is $Y = 0.28 - 0.32x$ ($n = 6$, one-tailed $P = 0.11$, $R^2 = 0.34$). The dotted line shows the 1 : 1 relationship.

zero in four of six systems (every case except terrestrial systems and marine plankton). The systems where predators had the greatest effects on herbivores were the same as those where plants responded most strongly (lentic and marine benthos, Fig. 1). Plants in the five aquatic systems collectively showed stronger responses to predators than those in terrestrial food webs ($P < 0.0001$ Table 2). System type explained 28.6% of the variation in the plant log ratio, and 35.0% of the variation in the herbivore response.

Although there were a number of methodological differences among the six systems, these did not appear to influence our results. We only included studies that measured plants as biomass or chlorophyll density (e.g. g/m^2) or percentage cover, however, some measured herbivores as density (e.g. number/m^2). We compared herbivore effect sizes in terms of numbers and biomass in the stream benthos where both measures were available. Although the biomass log ratio (mean = -0.02 , S.E. = 0.13, $n = 6$) was smaller than the abundance log ratio (mean = -0.40 , S.E. = 0.14, $n = 29$), the difference was quite small relative to the range in herbivore effect sizes observed among all six systems (Fig. 1). Including both measures of herbivore density therefore had minimal effects on our results. The durations of the experiments ranged from 6 to 8030 d, however, duration had no effect on the response to predators by either plants or herbivores (two-

Table 2 Planned orthogonal contrasts comparing plant and herbivore log ratios among systems. There were six systems, therefore we were able to make five contrasts. Our choice of contrasts reflects major divisions in habitat types.

Contrast	MS	F	P (two-tailed)
Herbivore log ratio			
Aquatic vs. terrestrial	12.07	9.33	0.0029
Plankton vs. benthos	9.07	7.01	0.0095
Plankton (lentic vs. marine)	0.13	0.10	0.7551
Benthos (marine vs. fresh)	0.40	0.31	0.5779
Benthos (lentic vs. stream)	55.42	42.85	< 0.0001
Plant log ratio			
Aquatic vs. terrestrial	6.37	16.94	< 0.0001
Plankton vs. benthos	4.11	10.93	0.0013
Plankton (lentic vs. marine)	2.19	5.83	0.0177
Benthos (marine vs. fresh)	4.45	11.84	0.0009
Benthos (lentic vs. stream)	0.74	1.97	0.1636

way ANOVA, $P > 0.1$ for effects of duration and its interaction with system type on plant and herbivore responses, Fig. 2). The number of replicates per treatment (range: 1–14) was also unrelated to both response metrics ($P > 0.1$).

Terrestrial studies were more likely than aquatic to use invertebrate predators (Table 1). Predator type had a marginal effect on the plant response ($P = 0.069$, Table 3). Across systems, vertebrate predators tended to have larger effects on plants (mean log ratio = 0.69, S.D. = 0.74) than invertebrates (mean plant log ratio = 0.33, S.D. = 0.53). There were nearly significant main and significant interactive effects of predator type and system type on the herbivore log ratio (Table 3), with vertebrate predators having greater effects than invertebrates (vertebrates: mean log ratio = -1.04 , S.D. = 1.56. invertebrates: mean log ratio = -0.72 , S.D. = 0.92). However, for both the plant and herbivore response, the differences among ecosystem types were much greater than those between vertebrate and invertebrate predators (Table 3). The lack of experiments with vertebrate predators and herbivores in terrestrial ecosystems highlights a major gap in the ecological literature. The terrestrial experiments included 14 grassland and four agricultural herbaceous plant communities; however, the plant and herbivore responses were very similar between the two groups (t -test, $P > 0.4$). Finally, a few terrestrial experiments sampled a more restricted subset of the plant community than the aquatic studies (e.g. only the dominant plants in the community, see Supporting Information). Because these studies tended to examine only the plants that were attacked by the herbivores of interest, our estimate of the plant effect size may be biased in favour of finding larger terrestrial cascades (Polis *et al.* 2000). Because our main hypothesis was that terrestrial systems show

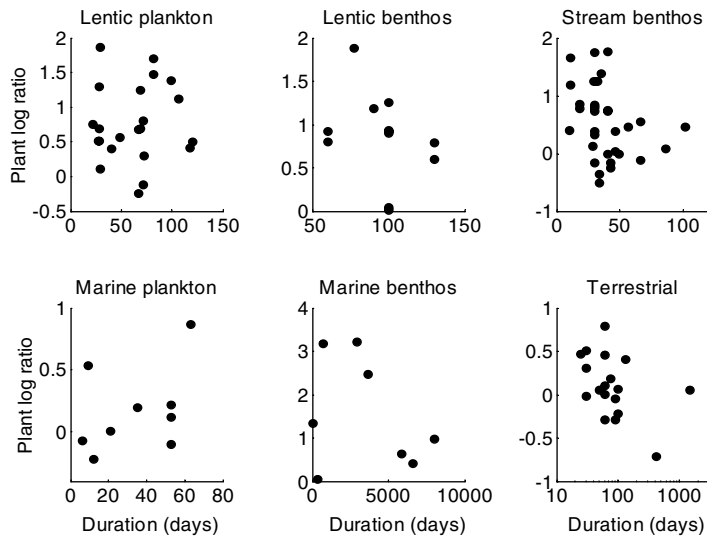


Figure 2 The effect size of predators (log ratio) on primary producers vs. experimental duration in each of the six ecosystems. A two-way ANOVA with duration and ecosystem type as factors found no significant effect of duration or its interaction with system type on the plant or herbivore log ratios ($P > 0.1$).

Table 3 Two-way ANOVA results for effects of predator type (vertebrate, invertebrate, or both) and system type on the herbivore and plant log ratios.

Source	MS	F	P (two-tailed)
Herbivore log ratio			
Predator type	3.18	3.02	0.054
System type	8.79	8.35	< 0.0001
Predator × system	4.39	4.17	0.002
Plant log ratio			
Predator type	1.01	2.76	0.069
System type	1.70	4.64	0.0008
Predator × system	0.27	0.73	0.601

weaker cascades, the taxonomic biases in the terrestrial data set render our test conservative. Although we used more stringent selection criteria than Schmitz *et al.* (2000), our estimate of the mean effect size of predators on terrestrial plant biomass (mean = 0.10, C.I. = 0.17) was comparable to theirs (mean = 0.22, C.I. = 0.11). Our results were therefore not strongly affected by our data selection criteria.

DISCUSSION

Our meta-analysis found that the biomass of primary producers showed weaker responses to predator removals in terrestrial food webs than in five aquatic systems. This result confirms earlier evidence that the strength of top-down control is greater in water than on land (Strong 1992; Polis & Strong 1996; Polis 1999; Halaj & Wise 2001). Although terrestrial predators had smaller effects on lower trophic levels, the differences among the five aquatic systems were often as great as those between wet and dry systems (Fig. 1). Surprisingly, some of the strongest cascades were

found in benthic habitats (both marine and lentic). The herbivores in these systems were snails and sea urchins (see Supporting Information), indicating that these organisms may be particularly susceptible to predators and have large impacts on their resources (benthic micro- and macroalgae). Terrestrial herbaceous plants showed weak responses to predation even though their herbivores were reduced to a similar degree to those in lakes and streams (Fig. 1). The small response by terrestrial plants therefore resulted from weakness in the link between plants and herbivores, not between herbivores and predators.

Two earlier meta-analyses of terrestrial trophic cascade experiments came to contrasting conclusions as to whether top-down control is weaker on land than in water. Schmitz *et al.* (2000) concluded that terrestrial cascades are as pronounced as those in freshwater pelagic systems. Halaj & Wise (2001) found that predators often affect plant damage and reproduction, but that effects on producer community biomass are generally weaker. Our results offer two potential insights into the causes of the apparent contradiction between these two studies. First, although there are many empirical examples of indirect effects of predators on some aspect of plant communities (e.g. plant growth, leaf damage, or species composition, McClaren & Peterson 1994; Krebs *et al.* 1995; Dyer & Letourneau 1999; Schoener & Spiller 1999; Berger *et al.* 2001; Terborgh *et al.* 2001), effects on plant community biomass have been shown much less often, and are generally weaker when they have been shown (Halaj & Wise 2001). We chose the biomass of the primary producer community as our metric for testing differences among systems because it is the focus of Hairston *et al.*'s (1960) original hypothesis. Using much of the same data as our study, Schmitz *et al.* (2000) found a mean log ratio for plant biomass of 0.22 (C.I. = 0.11). We

excluded a number of studies from Schmitz *et al.* that measured the response by a single plant species, and also added several newer studies. Our mean terrestrial response was 0.10 (C.I. = 0.17). The mean log ratio for primary producers in aquatic systems ranged from 1.54 (C.I. = 0.87) in marine benthos to 0.17 (C.I. = 0.22) in marine plankton. Thus, the data suggest that the effect sizes of aquatic predators on primary producer biomass are between 1.7 and 15.4 times greater than those in terrestrial ecosystems. Our data are in good agreement with other within-system meta-analyses, however, the earlier studies did not statistically test for differences between systems. Our analysis indicates that the differences between terrestrial and aquatic systems, and among aquatic systems, are both statistically and biologically significant (Table 2).

The second difference between our meta-analysis and earlier ones is that we considered a broader range of aquatic ecosystems. Schmitz *et al.* (2000) and Halaj & Wise (2001) only compared terrestrial data with freshwater plankton. Our data suggest that aquatic ecosystems in general, and not just lentic plankton, show stronger cascades than terrestrial herbaceous plant communities. Four of the five aquatic systems we considered (every case except marine plankton) found substantially greater predator effects on primary producers than those observed in terrestrial systems (Fig. 1). That we were able to find 84 aquatic experiments in five systems, and only 18 studies in terrestrial systems (confined entirely to grasslands and agricultural fields) highlights a major disparity in the ecological literature. Further study of the indirect effects of predation on the biomass of terrestrial plant communities is needed.

Although there were numerous methodological differences among studies in different ecosystems, these were not apparently responsible for the patterns we observed. Neither the experimental duration nor the number of replicates showed significant relationships with the plant or herbivore responses ($P > 0.1$, Fig. 2). This result held both within and across systems (i.e. there were no effects of either duration and replicate number, or their interactions with system type). One of the most important differences among systems lies in the generation time of the primary producers. In systems with unicellular producers (lentic plankton and benthos, marine plankton and stream benthos), most experiments lasted for several producer generations. In systems with multicellular producers (marine benthos and terrestrial), the experiments lasted from less than one generation to several generations (Fig. 2). However, the plant responses in the two systems with slowly reproducing plants ranged from the largest (marine benthos) to the smallest (terrestrial) in the survey. In addition, neither showed any apparent relationship between plant response and experimental duration (Fig. 2). Thus, there is no indication that differences in the length of the experiments

or the generation times of the producers were responsible for generating the difference in the strength of cascades between wet and dry ecosystems.

A number of differences between aquatic and terrestrial ecosystems may explain the tendency for stronger top-down control in water than on land. Strong (1992) proposed that trophic cascades are 'all wet' because phytoplankton are more uniformly palatable than terrestrial plants, and because terrestrial food webs are more 'reticulate' (i.e. have higher degrees of omnivory and trophic complexity). However, phytoplankton vary from edible to completely defended forms (Leibold 1989; Sommer 1989; Agrawal 1998; Tessier & Woodruff 2002). In addition, phytoplankton diversity is high relative to other plant communities (Hutchinson 1959; Sommer 1989; Leibold *et al.* 1997), and omnivory is common in both aquatic and terrestrial food webs (Diehl 1993; Vander Zanden & Rasmussen 1996). It is not clear that plant defences or diversity show consistent differences between aquatic and terrestrial systems, or that terrestrial food webs are intrinsically more 'complex' (Chase 2000). Nevertheless, our results support Strong's contention that the indirect effects of predators on plant biomass are greatest in aquatic ecosystems.

Several factors that are known to distinguish aquatic and terrestrial food webs include the following.

- 1 Body size ratios between herbivores and plants are generally larger with unicellular producers (periphyton or phytoplankton), which are common in aquatic systems but largely absent on land (Peters 1983; Hairston & Hairston 1993; Chase 2000).
- 2 Aquatic primary producers are more nutritious than terrestrial plants in that their elemental composition is more similar to that of their herbivores (Polis & Strong 1996; Cebrian 1999; Elser *et al.* 2000).
- 3 Terrestrial herbaceous and woody plants have lower rates of mass-specific biomass production than phytoplankton, benthic micro- and macro-algae, freshwater macrophytes or seagrasses (Cebrian 1999).
- 4 Herbivores consume a three-fold greater fraction of primary production in lentic plankton than in terrestrial food webs (Cyr & Pace 1993).

All of these differences may be expected to lead to more pronounced trophic cascades in water than on land (Shurin & Seabloom unpublished manuscript).

The smaller response by plants than herbivores in every system except streams indicates that the effects of predators often become attenuated as they are transmitted to lower trophic levels. The ratio of the plant-to-herbivore effect sizes ranged from -1.64 in streams to -0.18 in marine plankton, with a mean of -0.68. A 10-fold decrease in herbivore density therefore leads, on average, to just a 4.8-fold increase in producer biomass. In some systems (e.g.

marine plankton and terrestrial) substantial predator effects on herbivores led to negligible responses by the plant community. In others (e.g. lentic plankton, streams and marine benthos), the plant increases were of similar magnitude to the predators' effects on herbivores (Fig. 1). This suggests that variation in the strength of control of plants by herbivores is important for determining the magnitude of trophic cascades (Power 1992; Schmitz *et al.* 2000). Systematic differences in plant defences and tolerance to herbivory, compensatory growth, herbivore feeding efficiency or species turnover may determine whether the effects of predators on herbivores are dampened or amplified by the plant community.

Although we found large differences among food webs, system type explained only 28.6% of the variation in the effects of predators on plants, and 35.0% of the variation in the herbivore response. This suggests that factors that vary *within* systems (e.g. species diversity, behavioural responses, primary productivity, habitat structural complexity, measurement error) are more important for regulating the strength of cascades on those that vary *among* systems. In addition, although wet ecosystems generally showed stronger cascades than dry ones, there was considerable variation among the five aquatic ecosystems. Predator effects on herbivores were significantly greater in benthic than planktonic habitats, and in lentic benthos than in streams (Table 2). Plant responses were greater in benthos than in plankton, in freshwater plankton than marine plankton, and in marine benthos than freshwater (lentic and streams combined, Table 2). The five aquatic systems vary in a number of important biotic and abiotic features (e.g. plant size, physical structure, water velocity, etc.) that may affect the importance of top-down control.

Our meta-analysis confirmed that experimental studies of trophic cascades have found stronger responses to predator manipulations in aquatic than terrestrial food webs. Systematic variation in the strength of food web interactions has profound implications for the distribution of autotrophic and heterotrophic biomass among the earth's biomes, and for the control of trophic structure in different systems. Aquatic primary producers support higher consumption and production by herbivores than their terrestrial counterparts (Cyr & Pace 1993; Polis 1999). In contrast with terrestrial systems, aquatic food webs are characterized by large consumer-to-producer biomass ratios and inverted biomass pyramids. Our results indicate that real differences between aquatic and terrestrial communities also lead to stronger top-down influence over plant biomass in wet ecosystems. Human impacts on predators, for instance through hunting or fishing, may therefore have larger effects on primary producers and ecosystem processes in water than on land.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwell-science.com/products/journals/suppmat/ELE/ELE381/ELE381sm.htm>:

Appendix Reference for each study in the data set.

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