

Thomas Bell · William E. Neill · Dolph Schluter

## The effect of temporal scale on the outcome of trophic cascade experiments

Received: 12 March 2002 / Accepted: 5 November 2002 / Published online: 23 January 2003  
© Springer-Verlag 2003

**Abstract** The outcome of experimental manipulations in ecology should depend on the duration of the experiment. We tested this proposition by examining the results of published trophic cascade experiments in freshwater communities and the results of our own previously unpublished pond experiment. In particular, we analyze the results of 90 published trophic cascade experiments to test the prediction that the outcome of freshwater trophic cascade experiments, in which zooplanktivorous fish are either present or absent, depends on the duration of the experiment. We present evidence that there are quantitative differences in the strength of trophic cascades among different venue types (enclosure, mesocosm, pond, and lake), but that the strength of trophic cascades does not diminish with increasing experiment duration. Despite the large number of studies, there have been few replicated studies of trophic cascades for longer than a summer field season, and none for the time required to estimate the long-term result of press perturbations. We therefore present the results of a 4-year study of trophic cascades in experimental ponds, to test the predictions that the addition of the top predator results in a sustained increase in the phytoplankton biomass. We found that, as predicted by our literature review, there was no decline in the strength of the trophic cascade as the experiment progressed.

**Keywords** Biomanipulation · Experiment duration · Meta-analysis · Trophic level biomass

### Introduction

The outcome of experiments in community ecology should depend on their spatial and temporal scale (Levin 1992; Petersen et al. 1999; Solé et al. 1999), but few experiments have explicitly examined the role of scale on the outcome of a manipulation. Existing examples from terrestrial (Ives et al. 1993), aquatic (Sarnelle 1997), and riverine (Carignan and Planas 1994) ecosystems demonstrate that, when the same manipulation is applied at several scales, the duration of the experiment and the spatial extent of the study are often important in determining the outcome of the experiment. Consequently, it is necessary to evaluate whether ecological experiments are terminated too early to detect the effects of a manipulation. In the present study, we use the extensive literature that exists on aquatic trophic cascades, where both short- and long-term experiments are available, to examine the effect of temporal scale on the outcome of manipulations of the top trophic level.

There has been considerable interest over the last two decades in trophic cascades in both terrestrial (Schmitz et al. 2000, Halaj and Wise 2001) and aquatic (Persson 1999) systems. The interest has arisen both from the apparent generality of the response to adding or deleting the top predator, particularly in freshwater communities (Brett and Goldman 1996; Lawton 1999), and the applicability of this knowledge to controlling eutrophication through “biomanipulation” (Gophen 1990; Reynolds 1994; Drenner and Hambright 1999). The hypothesis that trophic cascades are important and common is most often tested by manipulating the top trophic level. Trophic cascades are implicated if the elimination of the top predator results in increased biomass two trophic levels below. Meta-analyses of trophic cascade experiments have shown that a large number of studies conform to the predictions of the trophic cascade hypothesis in aquatic (Brett and Goldman 1996), terrestrial (Schmitz et al. 2000), and intertidal (Menge 2000) communities. Shurin et al. (2002) have also recently compared the results of trophic cascade experiments across several ecosystem

T. Bell · W. E. Neill · D. Schluter  
Department of Zoology,  
University of British Columbia,  
6270 University Blvd., Vancouver,  
British Columbia, V6T 1Z4 Canada

T. Bell (✉)  
Department of Zoology,  
University of Oxford,  
South Parks Road, OX1 3PS Oxford, UK  
e-mail: thomas.bell@zoology.oxford.ac.uk

types. Although such meta-analyses confirm that trophic cascades are common in a variety of study systems, they also show a great deal of variability in the strength of the trophic cascade, that is, in the degree to which the predators affect herbivore and primary producer biomass.

Many hypotheses have been advanced to explain the observed variability in the strength of trophic cascades. Principal among these is that top-down effects interact with bottom-up effects to produce results that are not predictable unless nutrient dynamics are also taken into account (Oksanen et al. 1981; Polis 1994). Several other factors, especially spatial heterogeneity (Scheffer 1998), the prevalence of omnivory (Strong 1992; Diehl 1995), interference among predators (McCann et al. 1998) and heterogeneity in prey edibility (Leibold 1989; Bell 2002), have been suggested to modify the outcome of food web manipulations under certain conditions (Polis et al. 2000). However, it is not clear whether any of these factors is consistently important in determining the strength of trophic cascades. One factor that is rarely considered is the impact of scale on the outcome of these experiments. For example, the consistent top-down effects that occur with the addition of a trophic level might eventually disappear if there is delayed compensation by species that are adapted to avoiding predators (Osenberg and Mittelbach 1996). Furthermore, previous work has shown that the response ratios used in meta-analysis are often sensitive to experiment duration for a variety of ecological questions (Osenberg et al. 1997, 1999; Downing et al. 1999). They show that the conclusions drawn from short- and long-term experiments often differ considerably, and suggest weighting the log response ratio by the inverse of the experiment duration.

The purpose of this study is to test the hypothesis that the strength of trophic cascades diminishes with increasing experiment duration. We test the hypotheses in a quantitative literature analysis of aquatic trophic cascade experiments. We show that the analysis is confounded by the type of system in which the studies are conducted, with whole-lake experiments typically lasting much longer than mesocosm and enclosure experiments. Therefore, we also test the hypothesis that the strength of the trophic cascade declines with increasing experiment duration using data from a long-term (4-year) trophic cascade experiment in replicate pond communities.

## Literature analysis

### Materials and methods

We searched the literature for experiments in which zooplanktivorous fish were added or removed, and that recorded effects on zooplankton and phytoplankton biomass. We searched the Science Citation Index for articles containing the keywords: trophic cascade, biomanipulation, pond, enclosure, mesocosm, fish, and combinations thereof. Enclosure studies prior to 1996 were obtained from Brett and Goldman (1996), and supplemented with database searches. Whole-lake manipulation data were obtained primarily from the reviews of Leibold et al. (1997) and Hansson et al. (1998).

Systems were divided into enclosures (bags and lake enclosures and exclosures), mesocosms (cattle tanks, plastic pools, etc.), ponds, and lakes. Ponds were defined as man-made water bodies of similar size and shape each with an area <1 ha containing an evident benthic and limnetic invertebrate community. Lakes were defined as unreplicated water bodies with an area >1 ha. Unreplicated studies of lakes <1 ha were excluded from the analysis. We included whole-lake manipulations that reduced the abundance of zooplanktivorous fish by adding a piscivorous fish only when this method was accompanied by an additional methods of zooplanktivorous fish removal (e.g. netting, rotenone). The data were further divided into 3 duration categories: studies that lasted for a single summer (summer), for longer than a summer but less than a year (4–12 months) (1 year), or for longer than a year (>1 year).

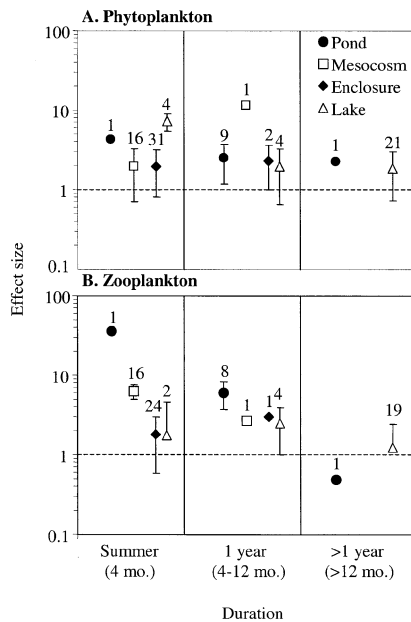
Data were taken from published figures using a digitizing tablet. A full list of the publications from which data were taken is included in the Appendix. Phytoplankton chlorophyll-*a* was used in preference to other measures of phytoplankton biomass. Biovolume and fluorescence were used when chlorophyll-*a* data were not available. Zooplankton dry weight was used to estimate zooplankton biomass. Zooplankton abundance was converted to dry weight using length-weight relationships, but typical weights of common zooplankton species (Hall et al. 1970; Wetzel and Likens 2000) were used when zooplankton size data were not available, as was most often the case. In some cases, crustacean or cladoceran biomass were used instead of total zooplankton biomass when data on the whole zooplankton community were lacking.

We calculated “effect sizes” to assess the impact of zooplanktivorous fish on zooplankton and phytoplankton biomass. The zooplankton effect size was the zooplankton biomass when the zooplanktivore was absent or at low density divided by the zooplankton biomass when the zooplanktivore was at high density. The phytoplankton effect size was the phytoplankton biomass at high zooplanktivore density divided by the phytoplankton biomass when the zooplanktivore was absent or at low density. Effect sizes were not weighted by the inverse of the variance, as is commonly done in meta-analysis (e.g. Gurevitch et al. 1992), because no among-replicate variance was available for unreplicated whole-lake experiments. The non-parametric Kruskal-Wallis test was used to test for differences in effect sizes among duration categories and types of venue because the Shapiro-Wilks test indicated that the data in many of the categories were non-normal ( $P>0.05$ ).

### Results

To assess whether the strength of trophic cascades was generally affected by experiment duration, we divided published studies into 3 duration categories (summer, 1 year, >1 year) (Fig. 1). Effect sizes (the magnitude of change resulting from the addition of zooplanktivorous fish) were calculated for each independent experiment. There was no significant difference among duration categories in phytoplankton effect sizes (Kruskal-Wallis:  $\chi^2_2=0.96$ ,  $P=0.62$ ). There was a difference among the zooplankton effect sizes (Kruskal-Wallis:  $\chi^2_2=11.44$ ,  $P=0.003$ ). Non-parametric multiple comparisons (Zar 1999) indicated that this difference was due to significantly smaller zooplankton effect sizes in the >1 year category than the summer category ( $Q_3=3.21$ ,  $P<0.005$ ) and the 1 year category ( $Q_3=2.59$ ,  $P<0.05$ ) categories. There was no difference between the summer and 1 year effect sizes ( $Q_3=0.10$ ,  $P>0.5$ ).

These initial comparisons are confounded by differences in typical venue between duration categories, with whole-lake experiments usually of longer duration than enclosure, mesocosm, and pond experiments. Whole-lakes were the only venue that had sufficient data from all three duration categories to warrant statistical tests that could control for the venue. There was a marginally non-significant difference in the phytoplankton effect sizes among the three duration categories when only the whole-lake data were used (Kruskal-Wallis:  $\chi^2_2=4.09$ ,  $P=0.08$ ) owing to a marginally non-significant decline between summer and >1 year effect sizes ( $Q_3=2.2$ ,  $P<0.1$ ) There was no significant difference



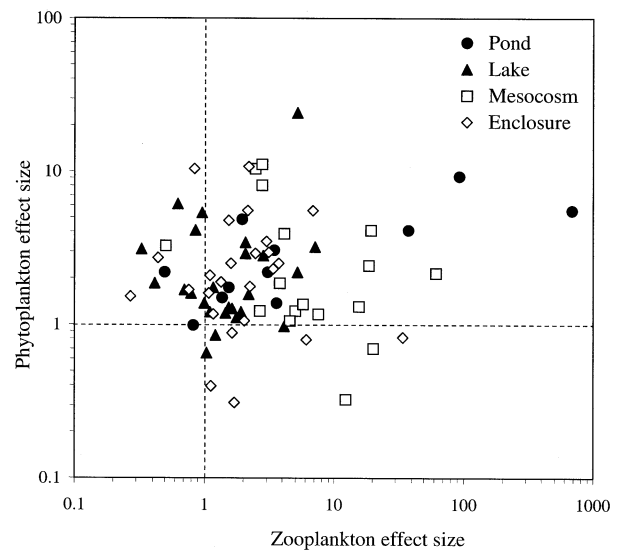
**Fig. 1** Mean ( $\pm$ SE) effect of fish on **A** phytoplankton and **B** zooplankton for published enclosure, mesocosm, pond, and whole-lake experiments that endured for up to 1 summer, 1 summer to 1 year, and longer than 1 year. Sample sizes are given above each data point. Datapoints above the *dashed line* (effect size  $>1$ ) conform to the predictions of the trophic cascade hypothesis (decrease in zooplankton, increase in phytoplankton with the addition of zooplanktivorous fish). References from which data were obtained are given in the Appendix

among the three categories for the zooplankton effect sizes (Kruskal-Wallis:  $\chi^2_2=2.49$ ,  $P=0.29$ ), although there were only two data points in the summer category.

We used Levene's Test to determine whether there was a difference in the variance of effect sizes among the duration categories. There was only weak evidence that the variance of the phytoplankton effect sizes differed among treatments (Levene's test:  $F_{2,88}=2.21$ ,  $P=0.12$ ). Pairwise Tukey-type multiple comparisons (Zar 1999) indicated a significant difference in the variance between the summer and  $>1$  year categories ( $q_{\infty,3}=4.12$ ,  $P<0.025$ ). The zooplankton data were more demonstrably heteroscedastic (Levene's test:  $F_{2,75}=3.25$ ,  $P=0.044$ ). This was because of a significant difference between the summer and  $>1$  year ( $q_{\infty,3}=4.27$ ,  $P<0.025$ ) and between the  $<1$  year and  $>1$  year categories ( $q_{\infty,3}=5.47$ ,  $P<0.001$ ). In sum, effect sizes were less variable in longer-term experiments.

We were also interested in whether there were differences in the phytoplankton and zooplankton effect sizes among the venue in which the experiments were performed. There was no difference in the effect of fish on phytoplankton biomass among studies that were conducted in different venue types (Fig. 2; Kruskal-Wallis test:  $\chi^2_3=0.65$ ,  $P=0.89$ ). There was a significant difference among zooplankton effects (Kruskal-Wallis:  $\chi^2_3=18.26$ ,  $P<0.0005$ ). This was due to a significantly larger zooplankton effect size in mesocosm studies compared to enclosure ( $Q_4=3.24$ ,  $P<0.01$ ) and whole-lake ( $Q_4=4.08$ ,  $P<0.001$ ) studies.

We also included both the duration of the study and the venue type in a two-factor ANOVA. Because the data in some of the categories were not normally distributed, we performed a nonparametric ANOVA using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf 1995). For the phytoplankton effect sizes, venue-type and the venue-type  $\times$  duration interaction were marginally non-significant ( $H_3=6.40$ ,  $P<0.1$  and  $H_4=8.11$ ,  $P<0.1$  respectively), but there was no main effect of duration ( $H_2=1.06$ ,  $P<0.75$ ). For the zooplankton data, there was a signifi-



**Fig. 2** Phytoplankton effect size (treatment/control) as a function of zooplankton effect size (control/treatment) from published experiments in ponds, mesocosms and enclosures and whole-lake manipulations. The data above and to the right of the *dashed lines* are in agreement with the predictions of the trophic cascade hypothesis (zooplankton and phytoplankton effect sizes  $>1$ ). References from which data were obtained are given in the Appendix

cant effect of venue-type ( $H_3=13.69$ ,  $P<0.005$ ), but duration and the duration  $\times$  venue-type interaction were not significant ( $H_2=2.69$ ,  $P<0.5$  and  $H_4=2.54$ ,  $P<0.5$  respectively).

#### Interpretation of the literature analysis

The results of the literature analysis suggest that there is no diminishment in the strength of trophic cascades in longer experiments. The data are difficult to interpret, however, because the analysis is confounded by the type of venue in which the studies are conducted; the great majority of short-term experiments are performed in replicated mesocosms or enclosures, whereas the multi-year experiments are performed almost exclusively in unreplicated lakes. To remedy this situation, we performed a long-term replicated whole-system study in experimental ponds, where we could test the prediction generated by the literature analysis.

## Pond experiment

### Materials and Methods

The experiment was conducted in 4 experimental ponds at the University of British Columbia, Canada from 6 July 1993 to 21 August 1997. The ponds are  $23 \times 23$  m<sup>2</sup>, and slope to a maximum depth of 3 m. They were built in 1991 and have not since been drained. The experiment consisted of two treatments. Zooplanktivorous fish (see below) were added to two of the four ponds, and the two other ponds were designated as controls. The control ponds used in this experiment have never contained fish. One of the ponds with fish had contained fish of the same species during 1992. Trapping removed most but not all of these fish 4 months prior to the beginning of this study.

Fish were introduced to two of the ponds during May 1993. We used a limnetic species of the threespine stickleback (*Gasterosteus* sp.), one of several populations endemic to five lakes (formerly six)

in British Columbia, Canada. Sticklebacks are ideal to use in such an experiment because they are cosmopolitan and common in most temperate countries, and because they have a relatively short generation time. Although the generation time has not been measured for Limnatics in the field, laboratory studies indicate that they typically breed and die within one year (D. Schluter, unpublished observations). The Limnetic species feeds primarily on open-water zooplankton in the wild, although adults, especially males, also consume littoral invertebrates during the spring breeding season (Schluter 1993).

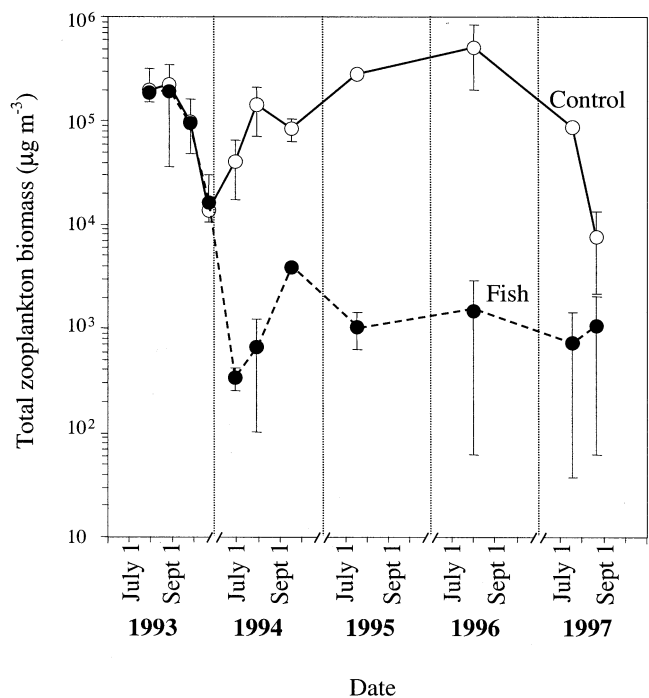
Parental fish were caught in Paxton Lake, British Columbia (49°43'N, 124°31'W). Eggs were obtained and fertilised in the laboratory (Hatfield and Schluter 1999; Vamosi et al. 2001). One thousand 8-week-old juvenile sticklebacks were introduced into one pond on 31 May 1993, and 689 into the other pond on 7 July 1993. The latter pond was supplemented with 161 2-week-old juveniles on 9 August 1993 for a total of 850 individuals (unexpected mortality in the laboratory precluded introducing the full 1,000 individuals). It is unlikely that differences in the initial populations could alter the outcome of the experiment because a short generation time would allow fish numbers to quickly adjust to available resources.

Fish were trapped using minnow traps over a 24-h period on 15 March 1994. Trapped fish were marked by clipping the first dorsal spine and released immediately after being marked. The same number of traps was used to recapture fish over the same amount of time 10 days following the marking. Because 76.3% of fish captured in the second trapping session were marked, the total number captured during the first session was a relatively accurate index of the total population size in the spring. For this reason, fish captured using the same number of traps in subsequent years were counted but not marked nor recaptured. For those years, we estimated the fish population size in each pond by assuming that the number caught in 24 h was equal to the same proportion of the total pond population that was captured in 24 h during March 1994. The same trapping procedure was followed in subsequent years on 6 June 1995, 11 April 1996, and 11 April 1997 to estimate stickleback population size. A total of 150 fish was removed from the ponds over the course of the experiment to analyze their gut contents.

Zooplankton were sampled periodically during the summer and early fall by pumping 15–75 l of water through 62  $\mu\text{m}$  Nitex netting. The zooplankton trapped on the netting were preserved in 5% formalin. Zooplankton were sampled haphazardly in areas devoid of macrophytes or mats of filamentous algae at a depth of 1 m. Zooplankton were enumerated and identified under a dissecting microscope. All of the organisms in the sample were counted unless zooplankton were very abundant in which case zooplankton were counted until 100 large (post-naupliar) crustacean zooplankton had been enumerated. Zooplankton biomass was calculated from abundance and length data using length-weight relationships from the literature (Bottrell et al. 1976; Downing and Rigler 1984).

Phytoplankton were sampled using a bilge pump from haphazard locations at 1 m and 2 m depths in areas clear of macrophytes and mats of filamentous algae during the summer and early autumn (May–October). Total phytoplankton biovolume did not differ between the two depths (paired  $t$ -test:  $t_{43}=1.2$ ,  $P=0.12$ ). All data were therefore averaged over depth prior to statistical analyses. Phytoplankton were placed in 250 ml glass jars, stained with approximately 3 ml Lugols solution, and stored until they were analyzed in the laboratory starting May 2000. Phytoplankton were settled in 10 ml chambers overnight (>18 h), and were then counted using an inverted microscope. Phytoplankton with a greatest linear dimension <10, <60, and >60  $\mu\text{m}$  were counted at magnifications of 600, 400, and 100x respectively. Forty fields of view were counted at each magnification, which was equal to 0.011, 0.19, and 0.73 ml of water respectively. Cell size and shape were recorded to calculate biovolume.

Repeated measures analysis of variance (ANOVAR) was used to estimate treatment effects over the course of the experiment



**Fig. 3** Mean ( $\pm$ SE) total zooplankton biomass in control ponds and ponds with fish. Error bars are asymmetric on a logarithmic scale

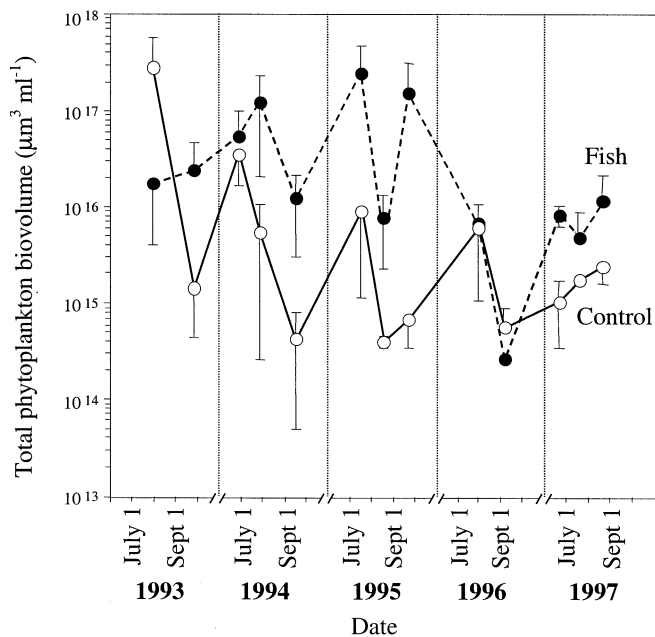
using SYSTAT 5.05. Data were log-transformed prior to statistical analyses to homogenize the variances.

## Results

Trapping confirmed that fish were persistent throughout the experiment (mean population size = 448.8 sticklebacks per pond), and that the two ponds did not differ in population size over the course of the experiment (paired  $t$ -test:  $t_4=0.60$ , n.s.). Unfortunately, the dates on which sticklebacks were trapped were not well matched with phytoplankton or zooplankton sampling dates, and so we were unable to relate fish density to plankton abundance.

Gut contents of the fish were also analyzed, although the sample size was too small to warrant statistical analyses. It was apparent, however, that the gut contents of the fish were highly variable. No single species consistently dominated stickleback diets. The small herbivorous cladoceran *Chydorus* was often numerically the most common item (mean percent of total gut organisms per fish for both ponds combined = 33.4%), but may have had little importance in supporting stickleback populations because of their low weight compared to larger cladoceran and copepod species. Calanoid and cyclopoid copepods, *Bosmina longirostris*, amphipods, *Diaphanosoma*, and ostracods were all numerically important during different years or in different ponds, but were never consistently important.

Zooplankton biomass was considerably higher in control ponds (ANOVAR:  $F_{1,2}=258.9$ ,  $P=0.004$ ) even though the initial average zooplankton biomass was almost identical in control ponds and ponds with fish for the four sampling dates at the outset of the experiment in 1993 (Fig. 3). There was both a significant Time effect ( $F_{10,20}=7.2$ ,  $P<0.0001$ ) and a significant Treatment  $\times$  Time interaction ( $F_{10,20}=3.9$ ,  $P=0.005$ ). The significant interaction term most likely results from the delayed effect of fish on zooplankton biomass over the first year of the experiment. The lower zooplankton biomass in ponds with fish was accompanied by a shift in zooplankton community structure. Ponds with no fish were dominated by larger zooplankton, especially large *Diaphanosoma*, calanoid copepods, and *Daphnia pulex*. Ponds with fish were



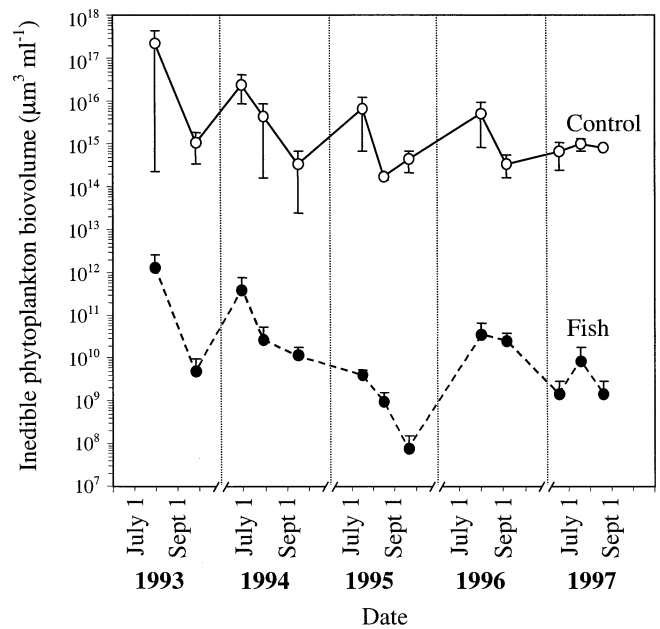
**Fig. 4** Mean ( $\pm$ SE) phytoplankton biovolume in control ponds and ponds with fish. *Error bars* are asymmetric on a logarithmic scale

dominated by smaller zooplankton species, especially *Bosmina* and *Chydorus*.

There was a higher total biovolume of phytoplankton in ponds with fish present compared to ponds without fish (ANOVAR;  $F_{1,2}=69.3$ ,  $P=0.014$ ) (Fig. 4). There was no significant time effect ( $F_{12,24}=1.0$ , n.s.), nor was there any interaction between time and treatment effects ( $F_{12,24}=0.6$ , n.s.). Phytoplankton were divided into two categories based on their edibility to common zooplankton. Phytoplankton greater than approximately 30–60  $\mu\text{m}$  are in general much less edible to even the largest zooplankton grazers than are smaller phytoplankton (Burns 1968; Vanderploeg 1981; Lehman and Sandgren 1985; McCauley and Downing 1985). When these size categories were analyzed separately (Fig. 5), further analysis indicated that the higher total phytoplankton biovolume in ponds with fish is the result of a higher contribution of small edible phytoplankton ( $<60 \mu\text{m}$  diameter) to the total phytoplankton biovolume (ANOVAR:  $F_{1,2}=123.3$ ,  $P=0.008$ ). In contrast, there was a higher biovolume of large inedible phytoplankton ( $>60 \mu\text{m}$  diameter) in the control ponds (Fig. 5; ANOVAR:  $F_{1,2}=85.65$ ,  $P=0.011$ ).

#### Interpretation of the pond experiment

The results from the experiment indicate that the zooplankton were consistently greater in ponds without fish for all data points subsequent to the first year of the study (Fig. 3). The phytoplankton response to zooplanktivorous fish additions was more variable. Overall, there was a greater phytoplankton biovolume in ponds with fish even though there was no difference (ANOVAR:  $F_{1,2}=0.11$ , n.s.) in the total phytoplankton biovolume during the first year of the experiment. The phytoplankton biomass was considerably higher in the pond with fish on all sampling dates except during the fourth year of the study 1996) when there was little difference in the phytoplankton biomass between the fish and control ponds (Fig. 4). By 1997, a higher phytoplankton biomass in ponds with fish had resumed. There was therefore little evidence for a damping of the trophic cascade at later dates.



**Fig. 5** Mean ( $\pm$ SE) abundance of inedible phytoplankton in control ponds and ponds with fish. *Error bars* are asymmetric on a logarithmic scale

## Discussion

We predicted that trophic cascades would be apparent in the majority of experiments, but that the strength of the trophic cascade would decline with increasing experiment duration. The results of our literature review indicate that, as predicted, trophic cascades occur in the great majority of studies, but that these results do not diminish over longer time scales. Rather, the analysis shows that trophic cascades are not only ubiquitous, but are also persistent. The results are consistent with recent meta-analyses, which also found no reduction in the strength of the trophic cascades with increasing experiment duration in aquatic and terrestrial systems (Schmitz et al. 2000; Shurin et al. 2002), although most of the experiments used in the analysis lasted for a single field season or less. Menge (1997) similarly found that a single year was most often sufficient to observe all of the indirect effects resulting from food web manipulations in rocky intertidal communities. The higher variability of phytoplankton and zooplankton effect sizes for very short experiments (one summer or less) suggests that researchers should remain cautious when extrapolating short-term results to longer time scales. A recent experiment (Attayde and Hansson 2001) demonstrated that even modest increases in the duration of their experiments (from 14 to 28 days) could considerably decrease the variability of the phytoplankton response to manipulations of higher trophic levels.

As with most meta-analyses, our analysis is confounded by the way in which researchers conduct experiments and by a presumed bias toward publishing positive results. For example, there is the possibility that experiments are terminated after reaching an effect size that the experi-

menters anticipate to be significant, which would result in no relationship between effect size and experiment duration. Conversely, it has previously been suggested (Osenberg et al. 1999) that it is possible to obtain a spurious correlation between effect size and experiment duration across studies because researchers that anticipate subtle (rather than strong) effects in their experiments are more likely to run their experiments for longer. Although we are unable to exclude either possibility, these criticisms might be unwarranted for our particular meta-analysis because the data are grouped into broad duration categories. As several authors have pointed out (Osenberg et al. 1997, 1999; Downing et al. 1999), it remains necessary to analyse and possibly to correct for differences in experiment duration prior to performing any meta-analysis.

The comparisons are obscured by differences in the type of venue in which the experiments are performed, with the duration of small-scale mesocosm and enclosure experiments typically much shorter than that of whole-lake manipulations. There is some evidence to suggest that phytoplankton effect size is lower for long-term manipulations when only whole-lake data are used, but the comparison might be biased by a low sample size of shorter experiments.

The results of the literature analysis also demonstrate that there are systematic differences in the results of trophic cascade experiments that depend on the type of venue in which the study is conducted. As such, it is in agreement with a number of other studies that the outcome to a manipulation depends on the type of venue (Coull and Chandler 1992; Schindler 1998; Skelly and Kiesecker 2001). We hypothesize that the effect of fish on zooplankton was higher in mesocosms because macrophytes are most often absent in mesocosms, but abundant in littoral zone enclosures and small lakes and ponds. Macrophytes act as zooplankton refuges from fish predation (Jeppesen 1998). Zooplanktivores might therefore be able to depress zooplankton to a greater extent in systems devoid of macrophytes, as is the case with many of the trophic cascade experiments in mesocosms.

Our experimental results broadly support the results of the literature analysis. Our pond experiment clearly demonstrate that the addition of a zooplanktivorous fish to replicate ponds results in a decrease in total zooplankton biomass and an increase in phytoplankton biovolume over prolonged periods. The results reported here are from the longest replicated experiment of aquatic trophic interactions of which we are aware. These results show that trophic cascades are maintained for 4 generations of the top predator despite a lower phytoplankton biomass in ponds with fish during the fourth year (1996) of the experiment. Such a prolonged experiment provides a good estimate of the long-term consequences of this press perturbation (Yodzis 1988). Although the models of Yodzis (1988) provide only a rough estimate of what would constitute a long-term experiment, few replicated studies approach the 2 generation mark, with the great majority of previous reports lasting for considerably less than a single generation of the top predator. Although the

duration of whole lake manipulations is typically longer than for smaller-scale experiments, few have run for the amount of time required to estimate the eventual outcome of the manipulation (Carpenter 1988; McQueen 1998).

In both our literature analysis and experiment, the zooplankton effect size failed to predict the phytoplankton effect size. We had assumed that this was because inedible phytoplankton compensated for losses in the edible phytoplankton, and in so doing, dampened the effect of zooplankton on the phytoplankton (Leibold 1989; Bell 2002). This hypothesis is supported to some degree by the rapid compensation by inedible phytoplankton in our pond experiment, but further work would be required to resolve this issue.

In sum, we conclude that, on average, short-term experiments are adequate to predict the long-term pattern of trophic level biomass. For aquatic trophic cascades, short-term experiments appear to be of adequate duration to predict longer-term patterns. Although we believe this conclusion is sound, it is evident that it will not and should not preclude further long term experiments in this area of research because unforeseen events often occur as experiments are lengthened (e.g. Ernest and Brown 2001). Enclosure experiments appear to mimic whole-system manipulations to a greater extent than mesocosms, but caution is warranted considering the previous poor track record of enclosure experiments in aquatic systems, the results of which often do not extrapolate to whole systems (Carpenter 1996; Schindler 1998).

Microcosms and mesocosms are the only systems in which many of the ideas in ecology can be tested because of the difficulty and expense of manipulating particular variables while holding all others constant over large spatial and temporal scales. Rather than dismissing the results of such experiments as inadequate at the spatial scale of a whole lake or forest, it is necessary to identify the way in which trophic cascades are altered because of venue alone. Such an approach has proved fruitful, for example in estimating the causes of differences in growth rates in larval anurans (Skelly and Kiesecker 2001), and the effect of *Daphnia* on microzooplankton (Sarnelle 1997). Similarly, an understanding of the effects of scale is crucial for understanding the importance of trophic cascades in terrestrial and marine ecosystems, where small-scale enclosure and exclosure experiments are often the only recourse.

**Acknowledgements** Thanks to D. Dolecki for collecting the plankton samples and for enumerating the zooplankton, and to numerous field assistants for collecting fish. A previous version of this manuscript was considerably improved by the comments of J. Richardson, D. Srivastava, the SOWD discussion group, O. Schmitz, C. Osenberg, and two anonymous reviewers. This work was supported by the Natural Sciences and Engineering Council of Canada.

## Appendix

Table 1 shows a full list of publications from which data were taken

**Table 1** Full list of publications from which data were taken

Source	Study type	Study length (days)	Phytoplankton effect (treatment/control)	Zooplankton effect (control/treatment)
Beklioglu and Moss (1995) <i>Freshw Biol</i> 33:497–509	Enclosure	25	1,096	213
Beklioglu and Moss (1996) <i>Freshw Biol</i> 36:315–325	Enclosure	27	1,068	082
Beklioglu and Moss (1998) <i>Aquat Ecol</i> 32:229–240	Enclosure	34	120	113
Bertolo et al. (1999) <i>Oecologia</i> 121:55–65	Enclosure	47	193	130
Bertolo et al. (1999) <i>Freshw Biol</i> 41:795–808	Enclosure	26	214	107
Bertolo et al. (2000) <i>Arch Hydrobiologia</i> 147:327–349	Enclosure	47	489	150
Christoffersen et al. (1993) <i>Limnol Oceanogr</i> 38:561–573	Enclosure	153	304	300
Crisman and Beaver (1990) <i>Hydrobiologia</i> 200:177–185	Enclosure	30	083	591
Crisman and Beaver (1990) <i>Hydrobiologia</i> 200:177–185	Enclosure	30	091	157
Crisman and Beaver (1990) <i>Hydrobiologia</i> 200:177–185	Enclosure	30	084	3,300
Crisman and Beaver (1990) <i>Hydrobiologia</i> 200:177–185	Enclosure	30	173	073
Leibold (1989) <i>Am Nat</i> 134:922–949	Enclosure	28	255	154
Lynch (1979) <i>Limnol Oceanogr</i> 24:253–72	Enclosure	40	297	237
Matveev et al. (2000) <i>Freshw Biol</i> 44:375–385	Enclosure	38	277	042
Mazumder et al. (1990) <i>J Plankton Res</i> 12:109–124	Enclosure	369	175	n.a. <sup>a</sup>
McQueen et al. (1992) <i>Arch Hydrobiologia</i> 125:1–24	Enclosure	96	157	026
Proulx et al. (1996) <i>Ecology</i> 77:1556–1572	Enclosure	72	109	196
Proulx et al. (1996) <i>Ecology</i> 77:1556–1572	Enclosure	72	356	290
Ramcharan et al. (1996) <i>CJFAS</i> <sup>b</sup> 53:2819–2828	Enclosure	67	164	105
Schindler (1992) <i>CJFAS</i> <sup>b</sup> 49:2498–2506	Enclosure	42	182	218
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	161	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	147	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	130	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	155	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	250	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	275	n.a. <sup>a</sup>
Slusarczyk (1997) <i>Hydrobiologia</i> 342/343:215–221	Enclosure	11	135	n.a. <sup>a</sup>
Stephen et al. (1998) <i>Freshw Biol</i> 39:699–713	Enclosure	35	258	364
Turner and Mittelbach (1992) <i>CJFAS</i> <sup>b</sup> 49:(1908–1915	Enclosure	47	235	324
Vanni and Findlay (1990) <i>Ecology</i> 71:921–937	Enclosure	89	567	660
Vanni and Layne (1997) <i>Ecology</i> 78:21–40	Enclosure	45	571	210
Vanni (1987) <i>Ecology</i> 68:624–635	Enclosure	31	032	165
Vanni (1987) <i>Ecology</i> 68:624–635	Enclosure	31	041	109
Byers and Vinyard (1990) <i>Oecologia</i> 83:352–357	Mesocosm	21	419	1,872
Byers and Vinyard (1990) <i>Oecologia</i> 83:352–7	Mesocosm	21	192	366
Byers and Vinyard (1990) <i>Oecologia</i> 83:352–357	Mesocosm	21	334	049
Byers and Vinyard (1990) <i>Oecologia</i> 83:352–357	Mesocosm	21	140	559
Drenner et al. (1990) <i>Hydrobiologia</i> 208:161–167	Mesocosm	21	250	1,800
Hansson et al. (1998) <i>Proc R Soc Lond</i> 265:901–906	Mesocosm	133	1,150	271
Hurlbert et al. (1972) <i>Science</i> 175:639–641	Mesocosm	103	1,061	237
Lancaster and Drenner (1990) <i>CJFAS</i> <sup>b</sup> 47:471–479	Mesocosm	28	071	1,956
Lazzaro et al. (1992) <i>CJFAS</i> <sup>b</sup> 49:1466–1473	Mesocosm	32	400	400
Nowlin and Drenner (2000) <i>Oecologia</i> 122:421–426	Mesocosm	11	109	436
Persson (1997) <i>Oikos</i> 79:137–146	Mesocosm	28	829	271
Richardson and Threlkeld (1993) <i>CJFAS</i> <sup>b</sup> 50:29–42	Mesocosm	26	033	1,189
Threlkeld (1988) <i>Limnol Oceanogr</i> 33:1362–1375	Mesocosm	35	220	5,926
Threlkeld (1988) <i>Limnol Oceanogr</i> 33:1362–1375	Mesocosm	40	126	259
Threlkeld (1988) <i>Limnol Oceanogr</i> 33:1362–1375	Mesocosm	45	134	1,508
Threlkeld (1988) <i>Limnol Oceanogr</i> 33:1362–1375	Mesocosm	55	127	480
Threlkeld (1988) <i>Limnol Oceanogr</i> 33:1362–1375	Mesocosm	62	121	736
Burke and Bayne (1986) <i>Prog Fish Cult</i> 48:177–183	Pond	203	224	297
Hall et al. (1970) <i>Limnol Oceanogr</i> 15:839–928	Pond	150	101	080
Hambright (1994) <i>Limnol Oceanogr</i> 39:897–912	Pond	820	224	048
Hambright et al. (1986) <i>CJFAS</i> <sup>b</sup> 43:1171–1176	Pond	90	154	134
Hurlbert and Mulla (1981) <i>Hydrobiologia</i> 83:125–151	Pond	271	958	9,003
Laws and Weisburg (1990) <i>Prog Fish Cult</i> 52:1–8	Pond	335	139	n.a. <sup>a</sup>
Meijer et al. (1990) <i>Hydrobiologia</i> 191:275–284	Pond	120	178	148
Milstein et al. (1988) <i>Aquat Fish Res</i> 19:127–137	Pond	120	420	3,625
Qin and Culver (1996) <i>Hydrobiologia</i> 321:109–18	Pond	40	142	344
Spencer and King (1984) <i>CJFAS</i> <sup>b</sup> 41:1851–1855	Pond	180	565	66,344

**Table 1** (continued)

Source	Study type	Study length (days)	Phytoplankton effect (treatment/control)	Zooplankton effect (control/treatment)
This study	Pond	1,460	313	337
Witeska (1995) <i>Acta Hydrobiologia</i> 37:121–129	Pond	168	500	190
Benndorf et al. (1988) <i>Limnologica</i> (19):97–110	Lake	1,825	068	101
Carpenter and Kitchell (1993) <i>The trophic cascade in lakes</i> Cambridge University Press	Lake	1,095	087	118
Donk et al. (1990) <i>Hydrobiologia</i> 200/201:275–301	Lake	1,095	350	200
Donk et al. (1990) <i>Hydrobiologia</i> 200/201:275–301	Lake	365	124	186
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	190	040
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–74	Lake	1,825	100	400
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	263	n.a. <sup>a</sup>
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	550	093
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	300	200
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	166	077
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	142	097
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	161	213
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	306	n.a. <sup>a</sup>
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	317	032
From Hansson et al. (1998) <i>Ecosystems</i> 1:558–574	Lake	1,825	171	069
Giussani et al. (1990) <i>Hydrobiologia</i> 200/201:357–366	Lake	730	129	159
Jeppessen et al. (1990) <i>Hydrobiologia</i> 200/201:205–227	Lake	1,095	177	114
Langeland (1990) <i>Hydrobiologia</i> 200/201:535–540	Lake	n.a. <sup>a</sup>	1,111	
Langeland (1990) <i>Hydrobiologia</i> 200/201:535–540	Lake	n.a. <sup>a</sup>	2,500	500
Langeland (1990) <i>Hydrobiologia</i> 200/201:535–540	Lake	n.a. <sup>a</sup>	625	061
Langeland (1990) <i>Hydrobiologia</i> 200/201:535–540	Lake	n.a. <sup>a</sup>	156	
Reinerstein et al. (1990) <i>CJFAS</i> <sup>b</sup> 47:166–173	Lake	1,095	420	083
Lynche et al. (1990) <i>Hydrobiologia</i> 200/201:251–261	Lake	365	329	692
McQueen et al. (1989) <i>Ecol Monogr</i> 59:289–309	Lake	1825	132	150
Persson et al. (1993) <i>Oikos</i> 66:193–208	Lake	1,095	114	170
Riemann et al. (1990) <i>Hydrobiologia</i> 200/201:241	Lake	1,095	121	141
Sondergaard et al. (1990) <i>Hydrobiologia</i> 200/201:229–240	Lake	730	224	500
Molen and Boers (1991) <i>Freshw Biol</i> 35:189–202	Lake	365	124	106
Vanni et al. (1990) <i>Nature</i> 344:333–335	Lake	365	291	276

<sup>a</sup> Not available<sup>b</sup> Canadian J Fish Aquat Sci

## References

- Attayde JL, Hansson L-A (2001) Press perturbation experiments and the indeterminacy of ecological interactions: effects of taxonomic resolution and experimental duration. *Oikos* 92:235–244
- Bell T (2002) The ecological consequences of unpalatable prey: Phytoplankton response to nutrient and predator additions. *Oikos* 99:59–68
- Bottrell HH, Duncan A, Gliwicz ZM, Grygierek E, Herzig A, Hillbright-Ilkowska A, Larsson P, Weglenska T (1976) A review of some problems in zooplankton production studies. *Norw J Zool* 24:419–456
- Brett MT, Goldman CR (1996) A meta-analysis of the freshwater trophic cascade. *Proc Natl Acad Sci USA* 93:7723–7726
- Burns CW (1968) The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnol Oceanogr* 13:675–678
- Carignan R, Planas D (1994) Recognition of nutrient and light limitation in turbid mixed layers: three approaches compared in the Paraná floodplain (Argentina). *Limnol Oceanogr* 39:580–596
- Carpenter SR (1988) Transmission of variance through lake food webs. pp. 119–135. In: Carpenter SR (ed) *Complex interactions in lake communities*. Springer, Berlin Heidelberg New York
- Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77:677–680
- Coull BC, Chandler GT (1992) Pollution and meiofauna: Field, laboratory, and mesocosm studies. *Oceanogr Mar Biol Annu Rev* 30:191–271
- Diehl S (1995) Direct and indirect effects of omnivory in a littoral lake community. *Ecology* 76:1727–1740
- Downing JA, Rigler FH (eds) (1984) *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell, Oxford
- Downing JA, Osenberg CW, Sarnelle O (1999) Meta-analysis of marine nutrient-enrichment experiments: variation in the magnitude of nutrient limitation. *Ecology* 80:1157–1167
- Drenner RW, Hambright KD (1999) Biomanipulation of fish assemblages as a lake restoration technique. *Arch Hydrobiol* 146:129–165
- Ernest SKM, Brown JH (2001) Delayed compensation for missing keystone species by colonization. *Science* 292:101–104
- Gophen M (1990) Biomanipulation: Retrospective and future development. *Hydrobiologia* 200/201:1–11
- Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. *Am Nat* 140:539–572
- Halaj J, Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? *Am Nat* 157:262–281

- Hall DJ, Cooper WE, Werner EE (1970) An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol Oceanogr* 15:839–928
- Hansson, L-A, Annadotter H, Bergman E, Hamrin SF, Jeppesen E, Kairesalo T, Luokkanen E, Nilsson P-Å, Söndergaard M, Strand J (1998) Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1:558–574
- Hatfield T, Schluter D (1999) Ecological speciation in sticklebacks: Environment-dependent hybrid fitness. *Evolution* 53:866–873
- Ives AP, Kareiva P, Perry R (1993) Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74:1929–1938
- Jeppesen E (1998) The structuring role of submerged macrophytes in lakes. Springer, Berlin Heidelberg New York
- Lawton JH (1999) Are there general laws in ecology? *Oikos* 84:177–192
- Lehman JT, Sandgren CD (1985) Species-specific rates of growth and grazing loss among freshwater algae. *Limnol Oceanogr* 30:34–46
- Leibold MA (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am Nat* 134:922–949
- Leibold MA, Chase JM, Shurin JB, Downing AL (1997) Species turnover and the regulation of trophic structure. *Annu Rev Ecol Syst* 28:467–494
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- McCann KS, Hastings A, Strong DR (1998) Trophic cascades and trophic trickles in pelagic food webs. *Proc R Soc Lond B* 265:205–209
- McCauley E, Downing J (1985) The prediction of cladoceran grazing rate spectra. *Limnol Oceanogr* 30:202–212
- McQueen DJ (1998) Freshwater food web biomanipulation: A powerful tool for water quality improvement, but maintenance is required. *Lakes Reservoirs Res Manage* 3:83–94
- Menge BA (1997) Detection of direct versus indirect effects: Were experiments long enough? *Am Nat* 149:801–823
- Menge BA (2000) Top-down and bottom-up regulation in marine rocky intertidal habitats. *J Exp Mar Biol Ecol* 250:257–289
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–261
- Osenberg CW, Mittelbach GG (1996) The relative importance of resource limitation and predator limitation in food chains. In: Polis GA, Winemiller KO (eds) *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York
- Osenberg CW, Sarnelle O, Cooper SD (1997) Effect size in ecological experiments: the application of biological models in meta-analysis. *Am Nat* 150:798–812
- Osenberg CW, Sarnelle O, Cooper SD, Holt RD (1999) Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80:1105–1117
- Persson L (1999) Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85:385–397
- Petersen JE, Cornwell JC, Kemp MW (1999) Implicit scaling in the design of experimental aquatic ecosystems. *Oikos* 85:3–18
- Polis GA (1994) Food webs, trophic cascades and community structure. *Aust J Ecol* 19:121–136
- Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? *Trends Ecol Evol* 15:473–475
- Reynolds CS (1994) The ecological basis for the successful biomanipulation of aquatic communities. *Arch Hydrobiol* 130:1–33
- Sarnelle O (1997) Daphnia effects on microzooplankton: Comparisons of enclosure and whole-lake responses. *Ecology* 78:913–928
- Scheffer M (1998) *Ecology of shallow lakes*. Chapman and Hall, London
- Schindler DW (1998) Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* 1:323–334
- Schluter D (1993) Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology* 74:699–709
- Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *Am Nat* 155:141–153
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette BB, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecol Lett* 5:1–7
- Skelly DK, Kiesecker JM (2001) Venue and outcome of ecological experiments: manipulations of larval anurans. *Oikos* 94: (198–208)
- Sokal RR, Rohlf, FJ (1995) *Biometry*. Freeman, New York
- Solé RV, Manrubia SC, Benton M, Kauffman S, Bak P (1999) Criticality and scaling in evolutionary ecology. *Trends Ecol Evol* 14:156–160
- Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754
- Vamosi SM, Hatfield T, Schluter D (2001) A test of ecological selection against young-of-the-year hybrids of sympatric sticklebacks. *J Fish Biol* 57:109–121
- Vanderploeg HA (1981) Seasonal particle-size selection by *Diatomus sicilis* in offshore Lake Michigan. *Can J Fish Aquat Sci* 38:504–517
- Wetzel RG, Likens GE (2000) *Limnological analyses*. Springer, Berlin Heidelberg New York
- Yodzis P (1988) The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508–515
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Englewood Cliffs, NJ.