The propagation of top-down and bottom-up signals
in heterogeneous aquatic food webs

by

THOMAS BELL

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Department of Zoology

The University of British Columbia
Vancouver, Canada

Date 12 September 2001

ABSTRACT

The two experiments described in this thesis attempt to identify the mechanisms that determine the biomass of trophic levels in freshwater communities. Early work in this field suggested that trophic level biomass is determined by resource supply and levels of predation. I present the results of two studies that investigate the impact of various other factors on the biomass of trophic levels. In the first study, I describe the short-term impact of prey (phytoplankton) edibility on the phytoplankton response to nutrient enrichment and the addition of a top (third) trophic level. The results suggest that the proportion of inedible phytoplankton in the community modifies the degree to which phytoplankton biomass is regulated by bottom-up (nutrient supply) or top-down (predation) forces. Compensation by inedible phytoplankton could therefore preclude the propagation of top-down signals in these communities. As a result, experiments over longer time scales might show a progressive weakening of top-down signals. In the second study, I therefore describe the results of a long-term (4-year) experiment in which zooplanktivorous fish are either present or absent. The results of this experiment, combined with the results of an extensive literature analysis, provide evidence that there is in fact no obvious decline in the strength of top-down signals with increasing experiment duration. The results do suggest, however, that the experimental results depend to some degree on the type of system in which the study is performed.

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CHAPTER I

Introduction and summary

1.1 TROPHIC LEVEL BIOMASS

Among the principal goals of ecology is to understand the mechanisms that determine the biomass of trophic levels. If the number of energy transfer steps determines the trophic position of an organism, then trophic levels are groups of organisms that all have the same or similar trophic positions. Although omnivores obscure definitions of trophic levels, some discrete trophic levels exist, including obligate primary producers and decomposers. The experiments presented in this thesis avoid some of the problems in defining trophic levels by concentrating on the primary producer trophic level. It is perhaps sufficient to note that simple food chain models perform surprisingly well, at least in aquatic systems, in predicting the response of food webs to various perturbations.

Much of the research on trophic levels has centred on whether trophic level biomass is principally determined by nutrient supply ("bottom-up") (Lindeman 1942), levels of predation ("top-down") (Hairston et al. 1960), or an interaction between the two (Oksanen et al. 1981). Theoretical and experimental work has shown that manipulating either the concentration of nutrients or the biomass of the topmost trophic level can alter the trophic level biomass of any trophic level. Although the top-down (Hairston et al. 1960, Fretwell 1977, Carpenter et al. 1985) and bottom-up (Lindeman 1942, White 1993) views were originally presented in opposition to each other, it is now widely recognized that such a dichotomy does not exist. If all else is equal, nutrients determine the potential biomass, and predation determines the actual biomass of any particular trophic level (Oksanen et al. 1981, Hunter and Price 1992). Trophic level biomass is therefore determined not only by resources and predation but also by the interaction between the

two. Recent reviews of the subject, however, have shown mixed results (Brett and Goldman 1997). Although it is evident that both resources and predation levels are important, it is also clear that there must be a number of other factors that modify the effect of these to determine the eventual trophic level biomass. Such factors include the structure of the physical environment (spatial heterogeneity), temporal heterogeneity in resource supply and predation levels, behavioural responses to alterations of the biotic and physical environment, the architecture of the food web in which interactions between organisms occur, as well as historical processes, chance, and several others (Polis et al. 2000). Much of this thesis deals with one of these factors, the architecture of the food web, and more particularly, the role of unpalatable prey in determining the biomass of primary producers in freshwater systems.

1.2 The consequence of inedible phytoplankton

Recent theoretical and laboratory studies have suggested that inedible or unpalatable prey modify the degree to which trophic levels are regulated by bottom-up or top-down forces such that primarily edible communities are regulated by predation and primarily inedible communities are regulated by resource supply. Despite the hypothesized importance of prey edibility, experiments have only rarely examined the response of primary producers to nutrient enrichment or the addition of a top trophic level following the reduction or elimination of inedible species. I performed two experiments in aquatic enclosures in which the prey (phytoplankton) had been manipulated to create treatments composed either nearly exclusively of only edible phytoplankton or with both

edible and inedible phytoplankton. In the first, the two types of phytoplankton community were subjected to either high or low nutrient concentrations. In the second, the two types of phytoplankton community were present in enclosures with either 2 or 3 trophic levels. I found that the impact of both the nutrients and the fish on total phytoplankton biomass was modified by the edibility of the phytoplankton community. Although enclosures with only edible phytoplankton were able to increase with enrichment, there was a greater overall phytoplankton biomass in enclosures with both edible and inedible phytoplankton. The addition of a third trophic level had a positive effect on phytoplankton biomass when only edible phytoplankton were present, but had no effect on phytoplankton biomass when both edible and inedible phytoplankton were present. These results therefore provide support for the hypothesis that the proportion of inedible phytoplankton determines the degree to which communities are regulated by top-down or bottom-up forces.

1.3 The effect of experiment duration

The results of the previous experiment demonstrate that inedible phytoplankton have a substantial impact on the propagation of top-down signals in aquatic systems. A number of long-term, usually unreplicated, experiments have further demonstrated that the removal of the third trophic level (zooplanktivorous fish) results in a net negative effect on phytoplankton biomass, but that the magnitude of the effect is dampened by a presumably concomitant increase in inedible phytoplankton. If inedible phytoplankton are able to completely compensate for losses in the edible phytoplankton, it is possible

that the "strength of the trophic cascade" (i.e. the degree to which the addition of a top trophic level alters the biomass of trophic levels below) will decline with increasing experiment duration. Despite attracting considerable interest, 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. I present the results of a 4-year study of trophic cascades in experimental ponds in which the top predator, a zooplanktivorous fish, was either present or absent. I tested two predictions of the trophic cascade hypothesis: (1) that the addition of the top predator (fish) results in a sustained increase in the primary producer (phytoplankton) biomass (2) that there is a relationship between the effect of fish on zooplankton and the effect of fish on phytoplankton. I tested the same two predictions on the results of 91 published trophic cascade experiments. I found that trophic cascades are important in determining trophic level biomass, but that there was no relationship between the effect of fish on zooplankton and the effect of fish on phytoplankton, both in my long-term experiment and my between-studies comparison. I present evidence that there are quantitative differences in the strength of trophic cascades among enclosure, mesocosm, pond, and whole-lake studies, but that the strength of trophic cascades does not diminish with increasing experiment duration.

CHAPTER II

The ecological consequences of inedible phytoplankton

2.1 INTRODUCTION

A number of studies have recently suggested that the impact of nutrients or predators on trophic level biomass is determined, at least in part, by the architecture of the food web (Hunter and Price 1992, Strong 1992, Persson et al. 2001). Food web architecture generally refers to the pattern and strength of feeding relations between organisms in a community. It includes such features as the edibility of prey species, the average connectance between species, and the prevalence of omnivory, shared predators, and intraguild predation (Holt and Lawton 1994, Morin and Lawler 1995, Holt and Polis 1997, Diehl and Feibel 2000).

There has been particular recent interest in the role of prey edibility in determining the biomass of trophic levels. The "edibility hypothesis" (Leibold 1989) focuses on how the presence of less-edible prey alter the predictions of food web theory. The model of Leibold (1989) and subsequent extensions explore the consequences of inedible species on the distribution of biomass (Grover 1995, Bohannan and Lenski 1999) and the stability (Abrams and Walters 1996, Genkai-Kato and Yamamura 1999, Huxel 1999) of trophic levels and of predator-prey systems. If a tradeoff between competitive ability and edibility is assumed, as appears to be the case for freshwater algae (Agrawal 1998) and terrestrial plants (Agren and Schemske 1993, Mutikainen and Walls 1995), then the models suggest that both the standing crop biomass and the stability or variability of trophic levels are altered by the presence of inedible species. In general, the models make the following predictions. First, that the inedible species (but not the edible prey) will increase with increasing resource levels in systems with 2 trophic levels.

Second, that edible species (but not inedible species) will increase with the addition of a third trophic level. Edible and inedible functional groups therefore play a critical role in communities because the balance between these two functional groups determines the degree to which the prey are regulated by bottom-up or top-down forces.

Comparative studies provide some support for these predictions. Such studies suggest that the communities composed of homogeneously edible prey (phytoplankton) are regulated by resource levels, and that prey communities heterogeneous in their edibility to predators are regulated by predation (McCauley et al. 1988). As predicted, lakes with greater nutrient concentrations also tend to have a greater proportion of inedible phytoplankton (Watson et al. 1988, 1992, Masson et al. 2000). Despite the obvious appeal of the theory in resolving the debate between proponents of the top-down and the bottom-up views, experimental tests of these hypotheses are rare. However, some examples exist from terrestrial (Schmitz 1994), aquatic (Leibold 1989, Hansson et al. 1998, Persson et al. 2001), and microbial systems (Bohannan and Lenski 1999). These studies manipulated resource levels and the presence of the top (third) trophic level and measured the response of the edible and inedible species. In general, these studies have provided only mixed support for the qualitative predictions of the models (above). Although enrichment and the addition of a third trophic level often results in increases in inedible and edible prey respectively (Leibold 1989, Hansson et al. 1998, Bohannan and Lenski 1999, Schmitz et al. 2000), a number of experiments report contrary patterns (Leibold 1989).

These correlational studies effectively document the consequences of nutrient and food web manipulations on the proportion of edible to inedible biomass. However,

notably absent are studies that investigate how the response to these manipulations is altered by also controlling prey edibility. Apart from studies using highly simplified microbial food webs (Bohannan and Lenski 1999, 2000), the experiments that have been performed to date therefore did not explicitly examine the role of prey edibility because it was not manipulated in the experiments. The present study is to my knowledge the first that investigates the consequences of inedibility by manipulating the edibility of phytoplankton in natural food webs of phytoplankton, zooplankton, and zooplanktivorous fish in aquatic enclosures. In particular, I examine the response of total phytoplankton biomass to nutrient and secondary consumer (zooplanktivorous fish) additions to food webs in which the proportion of inedible phytoplankton has been manipulated. The theory predicts (above) that top-down forces should regulate communities with a homogeneous prey trophic level (all prey edible), and bottom-up forces should regulate communities with a heterogeneous prey trophic level (edible and inedible species). This study therefore tests the following hypotheses: (1) There is a positive response to enrichment in heterogeneous but not homogeneous prey communities in systems with 2 trophic levels. (2) There is a positive response to the addition of a third trophic level in homogeneous but not heterogeneous communities.

2.2 METHODS

Study site and enclosures

The study was conducted in enclosures in an experimental pond at the University of British Columbia, Canada. The pond is 23 × 23 m and slopes to a maximum depth of 3.5 m. This pond has never contained fish since the ponds were built in 1991. Phytoplankton biomass in previous years was dominated by highly edible small flagellates, especially *Chlamydomonas* and *Cryptomonas*, although blooms of *Tetraedron* and small (<50 μm) dinoflagellates occasionally occurred. The larger phytoplankton, thought to be inedible to most zooplankton, are dominated by *Ceratium* and by filamentous blue-green (*Anabaena*) and green algae. Zooplankton biomass was dominated by *Daphnia pulex* and calanoid and cyclopoid copepods. Smaller cladocerans, such as *Chydorus*, *Diaphanosoma*, *Bosmina longirostrus*, and rotifers were also common, but most often contributed little to the total biomass.

The study was conducted in enclosures in the limnetic zone of an experimental pond from 13 July to 5 October 2000. The enclosures were constructed from UV-protected plastic bags suspended from a floating wooden frame. The bags were 1 m^2 by 2.5 m deep, and contained approximately 1000 L of water. They were closed to the sediment because the conditions were intended to mimic those of the pelagic zone of a small lake.

Experimental design

I created two types of phytoplankton community. Only edible phytoplankton were present in the first (*Homogeneous prey*), and both edible and inedible phytoplankton were

present in the second *(Heterogeneous prey).* To estimate the response of the phytoplankton community to nutrient enrichment, I added nutrients to half of the replicates (*High nutrients*) or left nutrients at ambient levels (*Low nutrients*). In a second experiment, zooplanktivorous fish were added to half of the *High nutrient* replicates (*3 trophic levels*) while the rest remained without fish *(2 trophic levels*). Although the study is treated as two separate experiments, the results of the *High nutrient+2 trophic level* treatment is used in both experiments (Table 2.1). Fish were also added to half of the *Low nutrient* replicates, but these were not used in the analysis of the results because of unexpected fish mortality. There were 2 replicates for each treatment combination.

Manipulation of the phytoplankton community

Previous studies have shown that phytoplankton larger than approximately 30 μm are for the most part inedible, or at the least highly unpalatable, to common zooplankton grazers (Burns 1968, Vanderploeg 1981, Lehman and Sandgren 1985, McCauley and Downing 1985). I therefore attempted to eliminate the inedible phytoplankton from half of the enclosures by filtering the water through fine netting as it was pumped into the enclosures. It is impossible in practice to eliminate all large (inedible) phytoplankton from the enclosures. The purpose of the manipulation was rather to create treatments with ambient and very low concentrations of inedible phytoplankton.

Water was added from the pond to the enclosures from 3 July to 12 July 2000. All water was first filtered through 202 μm Nitex netting to remove the macrozooplankton. In half of the enclosures (*Homogeneous prey*), the water was also filtered through 20 μm Nitex netting as it was added to the enclosures to remove the large inedible phytoplankton. In addition, approximately 2000 L of water in each enclosure containing

Homogeneous prey was passed through 20 μm netting subsequent to the initial filtering. I therefore estimate that the water in each enclosure was filtered 3 times before initiating the experiments. The macrozooplankton trapped on the 202 μm netting were subsequently introduced into the enclosures. Although the filtering procedure eliminates the smaller zooplankton (20-202 μm) from the *Homogeneous prey* enclosures, previous work in the same ponds (see Chapter III) suggests that small zooplankton have little effect on phytoplankton dynamics when large cladocerans are present in the system, as was the case in this study.

Size-fractionated phytoplankton samples were taken once every 10 days for the first 31 days of the experiment to check the efficacy of the phytoplankton manipulation. Water was withdrawn from the center of each enclosure and deposited in a jar using a hollow glass tube (1.5 m long, 18 mm diameter) fitted with a removable stopper. Two samples of 120 ml each were withdrawn from the jar. To estimate total phytoplankton biomass, one of the 120-ml samples was passed through a 25 mm diameter Whatman GF/F glass-fiber filter *in situ*. To estimate the contribution of the inedible phytoplankton (>30 μm), the same procedure was followed but the 120-ml sample was first passed through 30 μm Nitex netting. Both samples were incubated in 95% acetone overnight (>18 h) at 4C. Phytoplankton Chl *a* was estimated using the fluorometric technique (Lind 1979). The contribution of the edible phytoplankton (<30 μm) was obtained by subtracting the >30 μm Chl *a* from the total phytoplankton Chl *a*.

Analysis of these samples indicated that the filtering procedure described above was successful in creating treatments with a higher biomass of edible phytoplankton, and that the manipulation was sustained throughout the experiment. Small edible

phytoplankton contributed on average 93.1% of the total phytoplankton biomass in *Homogeneous prey* enclosures, and only 51.7% in *Heterogeneous prey* enclosures (Figure 2.1). Repeated measures analysis of variance (ANOVA) confirmed that this difference was statistically significant ($F_{1,10} = 84.2$, $P < 0.0005$). There was furthermore no difference in the total phytoplankton biomass between *Homogeneous* and *Heterogeneous prey* enclosures immediately following the manipulation of the phytoplankton community ($F_{3,4} = 0.51$, $P = 0.69$).

***Experiment 1**: The effect of enrichment*

The experiment was initiated on 24 July 2000 when 0.175 μg L^{-1} KH_2PO_4 and 3.883 μg L^{-1} $NaNO_3$ were added to the *High nutrient* enclosures. The nutrients were first dissolved in 5 L of water from the enclosure into which the nutrients were being added. The water in the enclosures was mixed briefly immediately following the nutrient addition to ensure an initial even distribution of the nutrients within the enclosures. No nutrients were added to the *Low nutrient* enclosures, but these enclosures were also briefly mixed. Phytoplankton were usually sampled twice weekly beginning 20 July 2000. Total phytoplankton biomass was measured as described in the previous section.

Zooplankton were sampled near the beginning (7 August 2000) and conclusion (20 September 2000) of the experiment. I used the same glass tube to collect the zooplankton as was used to collect the phytoplankton. Fifteen liters of water were obtained from each enclosure and was sieved through 100 μm Nitex netting. The zooplankton trapped on the netting were then placed in scintillation vials in 95% ethanol. Zooplankton were enumerated and measured under a dissecting microscope after the

conclusion of the experiment. Zooplankton biovolume was estimated from the maximum length and width of each individual. Because the 100 μm netting is unreliable for sampling the smallest zooplankton (e.g. rotifers and copepod nauplii), total zooplankton biomass was estimated as the biomass of the macrozooplankton (post-naupliar cladocerans and copepods). Although additional zooplankton samples were also obtained over the course of the experiment from smaller samples of water (2 L), insufficient zooplankton were obtained per sample to accurately estimate zooplankton density. These samples were therefore not included in the analysis.

***Experiment 2**: The effect of zooplanktivorous fish additions*

I used the Limnetic species of the threespine stickleback (*Gasterosteus* sp.), a zooplanktivorous fish (Schluter 1993), as the top predator trophic level. Parental fish were captured from Paxton Lake, British Columbia, Canada (49°43'N, 124°31'W) during May 2000. Eggs from a single female were fertilized with the sperm from a single male in the laboratory. The progeny were raised in the laboratory for 6 weeks before being added to the appropriate enclosures at the initiation of the experiment (4 September 2000). Five individuals (mean weight = 88.9 mg, mean standard length = 21.1 mm) were added to each of the appropriate enclosures. The fish added to each enclosure were drawn haphazardly from the available stock. There was no difference in the mean weight of the fish added to each enclosure (ANOVA: $F_{3,16} = 0.83$, $P = 0.50$). Although the addition of predators was 46 days after the initial phytoplankton manipulation, there was little change in the proportion of edible phytoplankton in the *Homogeneous prey* enclosures (Figure 2.1), indicating that the manipulation of the phytoplankton community persisted throughout the experiment.

The fish were transported to the enclosures and allowed to acclimatize to pond temperatures overnight in plastic bags half filled with aquarium water before being added to the enclosures. They were removed from the enclosures at the conclusion of the experiment first using minnow traps overnight for 3 consecutive nights, and then by adding rotenone ($C_{23}H_{22}O_6$). Phytoplankton and zooplankton sampling methods were the same as for **Experiment 1**. Phytoplankton were sampled every 10 days beginning 9 days prior to the addition of the fish (26 August 2000).

Analyses

For **Experiment 1**, I tested for differences in the phytoplankton biomass among the treatments using repeated measures analysis of variance (ANOVAR), where the phytoplankton community (*Homogeneous* and *Heterogeneous prey*) and nutrient concentration (*High* and *Low*) were the dependent variables. To investigate more general patterns in the data, I calculated the grand mean across the time series for each treatment, and compared treatments using a factorial ANOVA. For **Experiment 2**, I wanted to test the hypothesis that zooplanktivorous fish had a greater positive effect on phytoplankton biomass in the *Homogeneous prey* treatment then in the *Heterogeneous prey* treatment. Phytoplankton biomass was therefore converted to effect sizes by dividing the phytoplankton biomass in each replicate enclosure with 3 trophic levels by the phytoplankton biomass in the appropriate controls (*2 trophic levels*). The data were then standardized for differences between enclosures prior to the start of the experiment by subtracting the difference between the treatment (*3 trophic levels*) and the appropriate control (*2 trophic levels)* for each data points in the time series. The resulting time series

represents the effect of fish on phytoplankton biomass. The time series were compared using repeated measures ANOVA. All statistical analyses were performed on log-transformed data to homogenize the variances. The statistics were computed using SYSTAT 5.05.

2.3 RESULTS

Experiment 1: *The effect of enrichment*

In this experiment, I examined the effect of enrichment on the two types of phytoplankton communities. I predicted (see Introduction) that phytoplankton biomass would increase in the *Heterogeneous prey* enclosures but not in the *Homogeneous prey* enclosures. The prediction was confirmed to some degree because there was a marginally non-significant increase in the phytoplankton biomass with enrichment in the *Homogeneous prey* treatment (ANOVAR: $F_{1,2}$ = 13.6, P = 0.065), and a significant increase in the *Heterogeneous prey* treatment (ANOVAR: $F_{1,2}$ =47.6, P = 0.020) (Figure 2.2). For the latter, there was also a significant Time × Nutrient interaction (ANOVAR: $F_{18,36}$ = 2.3, P = 0.018). However, when the status of both the phytoplankton community (*Homogeneous* and *Heterogeneous prey*) and the nutrient concentration (*High* and *Low*) were included in a repeated measures analysis of variance, the nutrient concentration but not the edibility of the phytoplankton community had a significant effect on the total phytoplankton biomass (Table 2.2). The significant Time × Nutrient × Edibility interaction suggests that the edibility of the phytoplankton community does play some role in the response of the total phytoplankton biomass to enrichment.

I averaged the phytoplankton biomass across the time series of each enclosure to look at coarser trends in the data. The data show (Figure 2.3) that as predicted (above), the biomass of the *Heterogeneous prey* phytoplankton communities was able to increase substantially with enrichment to 3.0-times the biomass in enclosures that did not receive any nutrients. Contrary to the prediction, however, the *Homogeneous prey* phytoplankton communities were also able to increase with enrichment to 3.6-times the biomass without nutrient inputs. When both nutrients and phytoplankton edibility are included in a fully factorial ANOVA, both nutrients ($F_{1,5}$ =28.71, P = 0.006) and phytoplankton edibility ($F_{1,5}$ = 8.35, P = 0.045) had a significant effect on total phytoplankton biomass, but there was no interaction between the two ($F_{1,5}$ = 1.07, P = 0.40). However, there was no difference in the phytoplankton biomass between *High nutrients+Homogeneous prey* and *Low nutrients+Heterogeneous prey*, suggesting that the growth of the phytoplankton in the *Homogeneous prey* might be constrained by higher zooplankton grazing rates. However, the absence of a difference between the two *High nutrient* treatments (*Homogeneous* and *Heterogeneous prey*) indicates that zooplankton could not have greatly affected the phytoplankton biomass in *Homogeneous prey* enclosures.

If nutrient enrichment results in a higher density of edible phytoplankton, then zooplankton density should also increase with enrichment. There was no difference in the total zooplankton biomass among the treatments near the beginning (7 August 2000) of the experiment (ANOVA: $F_{3,4}$ = 1.22, P = 0.41). As predicted, manipulation of the phytoplankton community and nutrient concentrations resulted in a difference in the zooplankton biomass among the treatments near the conclusion of the study (ANOVA: $F_{3,4}$ = 13.73, P = 0.014) because of a significantly higher zooplankton biomass in the

enriched *Homogeneous prey* enclosures (Figure 2.4). There is therefore a significant interaction between nutrient levels and phytoplankton community structure when the data are included in a factorial ANOVA ($F_{1,4} = 12.0$, $P = 0.026$).

Experiment 2: *The effect of zooplanktivorous fish additions*

As expected, there was a lower zooplankton biomass in enclosures with 3 trophic levels ($t_6 = 2.87$, $P = 0.028$), presumably because of grazing by zooplanktivorous fish. I predicted (see Introduction) that the addition of zooplanktivorous fish would have a positive effect on phytoplankton biomass in both *Homogeneous* and *Heterogeneous prey* treatments, but that this effect would be more pronounced in the *Homogeneous prey* enclosures. There was no significant effect of fish on phytoplankton biomass in the *Homogeneous prey* enclosures (ANOVAR: $F_{1,2} = 3.57$, $P = 0.20$) but there was a significant Time effect ($F_{3,6} = 28.3$, $P = 0.001$) and Time × Treatment interaction ($F_{3,6} = 8.9$, $P = 0.013$) (Figure 2.5). The biomass of phytoplankton was higher (marginally non-significant) in enclosures with fish for the *Heterogeneous prey* treatment (ANOVAR: $F_{1,2} = 15.02$, $P = 0.061$), although this appeared to be due to initial differences between treatment (*3 trophic levels*) and control (*2 trophic levels*) enclosures (Figure 2.5).

After calculating phytoplankton effect sizes and standardizing for initial differences between treatments and controls (Figure 2.6), there was no significant difference between phytoplankton effect sizes in the *Homogeneous* and *Heterogeneous prey* treatments (ANOVAR: $F_{1,2} = 0.52$, $P = 0.54$). However, the significant Time × Treatment interaction ($F_{3,6} = 50.0$, $P < 0.0005$) suggests that the qualitative divergence between the *Homogeneous* and *Heterogeneous prey* effect sizes as the experiment

progressed is real. Pairwise comparisons at each sampling date indicated that there was a significantly higher effect of zooplanktivorous fish on phytoplankton biomass in the *Homogeneous prey* enclosures on the final sampling date (Tukey test: $q_{10,5} = 2.25$, $P = 0.032$), but there was no significant difference on any of the other sampling dates. I therefore conclude that the fish had a positive effect on phytoplankton biomass, but perhaps only in the *Homogeneous prey* enclosures. Further, the hypothesis of a greater effect of fish in *Homogeneous prey* enclosures is upheld, at least by the conclusion of the experiment.

2.4 Discussion

The experiments in this study confirm the suggestions of previous authors (Leibold 1989, Agrawal 1998) that prey (phytoplankton) edibility, here represented as phytoplankton size, can have considerable effects on the dynamics of the phytoplankton trophic level. The results of **Experiment 1** demonstrate that the phytoplankton respond differently to nutrient enrichment in the two types of phytoplankton community (*Homogeneous* and *Heterogeneous prey*). Theory predicts that prey biomass should increase with enrichment in 2-trophic level systems only if some of the prey are inedible (Leibold 1989, Kretzschmar et al. 1993, Bohannan and Lenski 2000) or unpalatable (Grover 1995). If there are only edible prey, any increases in primary production would simply result in increases in primary consumer biomass as they offset increases in their prey. If inedible phytoplankton are present, not only are edible algae susceptible to grazing losses, but the inedible algae are at a competitive advantage because they act as

nutrient "sponges" by sequestering the available nutrients (Watson et al. 1988, Bohannan and Lenski 1999), which might therefore lead to further reductions in the biomass of the edible phytoplankton.

As predicted, there was an increase in the phytoplankton biomass with enrichment in the *Heterogeneous prey* enclosures. Contrary to the predictions, there was also an increase in the phytoplankton with enrichment in the *Heterogeneous prey* enclosures, and as a result there was no interaction between nutrients and prey community categories. Despite the absence of an interaction, there was a differential effect of enrichment on the two types of phytoplankton community that was manifest in an overall higher total phytoplankton biomass in enclosures with heterogeneous prey. This might occur if the two size fractions not only differ in their edibility to zooplankton grazers but also in their resource requirements. The models that have investigated the effects of prey edibility assume that phytoplankton differing in their edibility have identical resource requirements. Such an assumption may be unrealistic, especially if phytoplankton with anti-predator traits, such as thicker cell walls, require different ratios of the common micronutrients, as is the case for many inedible blue-green algae (MacKay and Elser 1998).

The mechanism by which phytoplankton were able to increase in the *Homogeneous prey* enclosures despite concomitant increases in the zooplankton also remains unclear. It is possible that the zooplankton were not given sufficient time to respond to increases in edible phytoplankton biomass, but experiments show that zooplankton are able to approach equilibrium densities over comparable time scales (Walters et al. 1987, Attayde and Hansson 2001). Alternatively, increased interference

among zooplankton with increased zooplankton densities (McCann et al. 1998), including interference competition and intraguild predation, could also lead to the observed increase in edible phytoplankton with enrichment. Finally, it is also possible that small but inedible algae became abundant in the *Homogeneous prey* enclosures. Unfortunately, the methods used during the experiment were insufficient to account for this possibility. Further work would be required to distinguish among these hypotheses.

There is now considerable evidence that top-down forces are important in regulating trophic level biomass in aquatic systems (Brett and Goldman 1996). There is a great deal of variability, however, in the degree to which phytoplankton biomass is affected by the trophic levels above. Several authors have suggested that the strength of trophic cascades are contingent on the degree of heterogeneity, or functional complexity, in the lower trophic levels (Hunter and Price 1992) such that trophic cascades are common in "simple" aquatic food webs, but rare in more complex terrestrial systems (Polis 1994). It is evident that the addition of a third trophic level should have little effect on lower trophic levels if the primary producer biomass is dominated by organisms that are inedible to the primary consumers. Primary producer communities that are homogeneous in their edibility to primary consumers should therefore be more tightly regulated by top-down forces than heterogeneous communities.

For **Experiment 2**, I therefore predicted (see Introduction) that there would be a greater response to the addition of a third trophic level in the *Homogeneous prey* treatment. The results from this study uphold this prediction. I demonstrated that, by the conclusion of the study, the magnitude of the effect of the secondary carnivore (zooplanktivorous fish) on primary producer biomass depends on the edibility of the

primary producer trophic level. Results from previous enclosure experiments have been restricted to the observation that inedible phytoplankton commonly, but not always, increase with increases in zooplankton biomass (Leibold 1989) and therefore dampen the trophic cascade. Similarly, several hypotheses based on comparative data have suggested that the degree to which top-down forces regulate trophic levels depends on nutrient concentrations (Coley et al. 1985, McQueen et al. 1986, Elser and Goldman 1991). Although there is some debate as to whether trophic cascades are important in oligotrophic (nutrient-poor) lakes, there is general agreement that trophic cascades are weak in nutrient-rich aquatic systems because they are dominated by inedible phytoplankton (Watson et al. 1988, 1992). Interestingly, terrestrial plants appear to exhibit the opposite pattern, with decreased plant defense in nutrient-rich environments (Coley et al. 1985). Comparisons between terrestrial and aquatic systems are complicated, however, for example by differences in plant and herbivore life-history strategies between terrestrial plants and phytoplankton (e.g. perenniality, size differences between primary producers and herbivores) as well as by differences in the ratio and absolute concentration of available nutrients, which might influence the relative cost of defense. Unfortunately, comparative studies cannot separate the effects of nutrient concentration from phytoplankton edibility and other covariates of lake nutrient concentrations (such as lake size) on the strength of the trophic cascade. To my knowledge, **Experiment 2** is the first manipulative experiment to demonstrate that phytoplankton edibility alone can have a strong impact on the strength of trophic cascades.

Table 2.1

Summary of the experimental design for the 2 experiments in this study. Each cell is a replicate (2 replicates for each treatment combination).

	Low nutrients		High nutrients			
	2 trophic levels		2 trophic levels		3 trophic levels	
Homogeneous prey	1	2	3	4	5	6
Heterogeneous prey	7	8	9	10	11	12
	Experiment 1		*Experiment 2*			

Table 2.2

Results of a repeated measures ANOVA to determine the effect of nutrient enrichment (*High* and *Low nutrients*) and of the phytoplankton community (*Homogeneous* and *Heterogeneous prey*) on total phytoplankton biomass.

	Source of Variation	*F*	Num. df	Den. df	*P*
Between subjects	Nutrients	14.55	1	4	0.019
	Edibility	1.01	1	4	0.372
	Nutrient × edibility	0.49	1	4	0.523
Within subjects	Time	5.16	18	72	<0.0005
	Time × nutrients	2.22	18	72	0.009
	Time × edibility	0.76	18	72	0.740
	Time × nutrient × edibility	1.94	18	72	0.026

Figure 2.1: Mean percent of the total phytoplankton biomass (Chl *a*) in the edible (<30 μm) fraction for the *Homogeneous* and *Heterogeneous prey* enclosures. Error bars are the standard error of 4 enclosures for each sampling date.

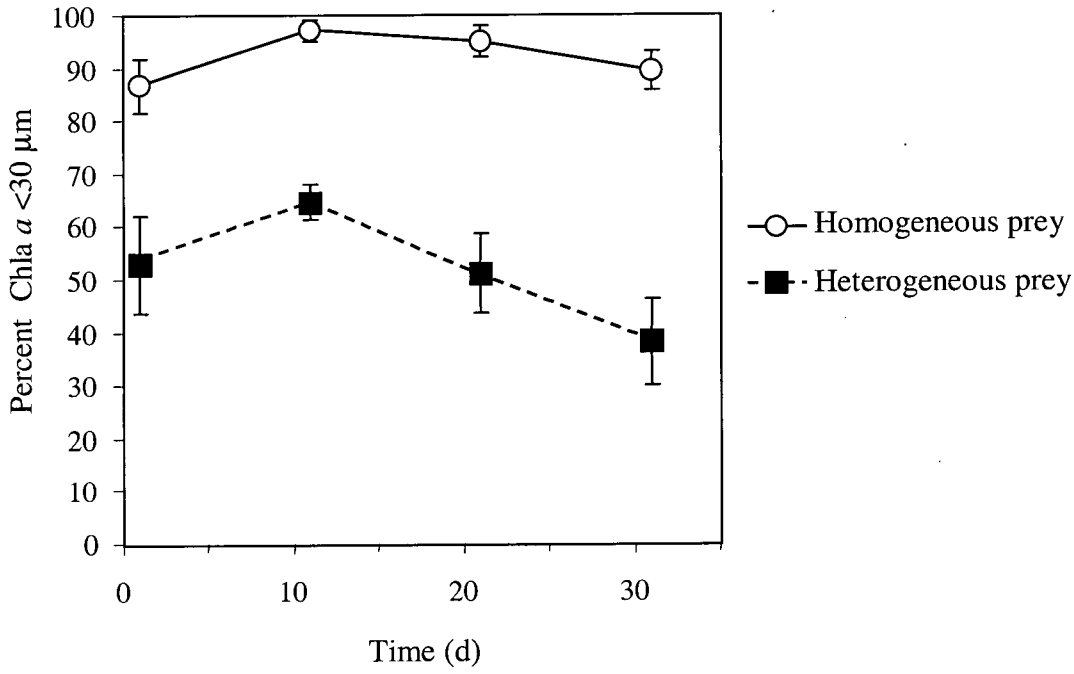
Percent Chla a <30 µm
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
Time (d)
Homogeneous prey
Heterogeneous prey

Figure 2.1

Figure 2.2: Mean phytoplankton biomass (±SE) in the *High* and *Low nutrient* enclosures for *Homogeneous* and *Heterogeneous prey* phytoplankton communities.

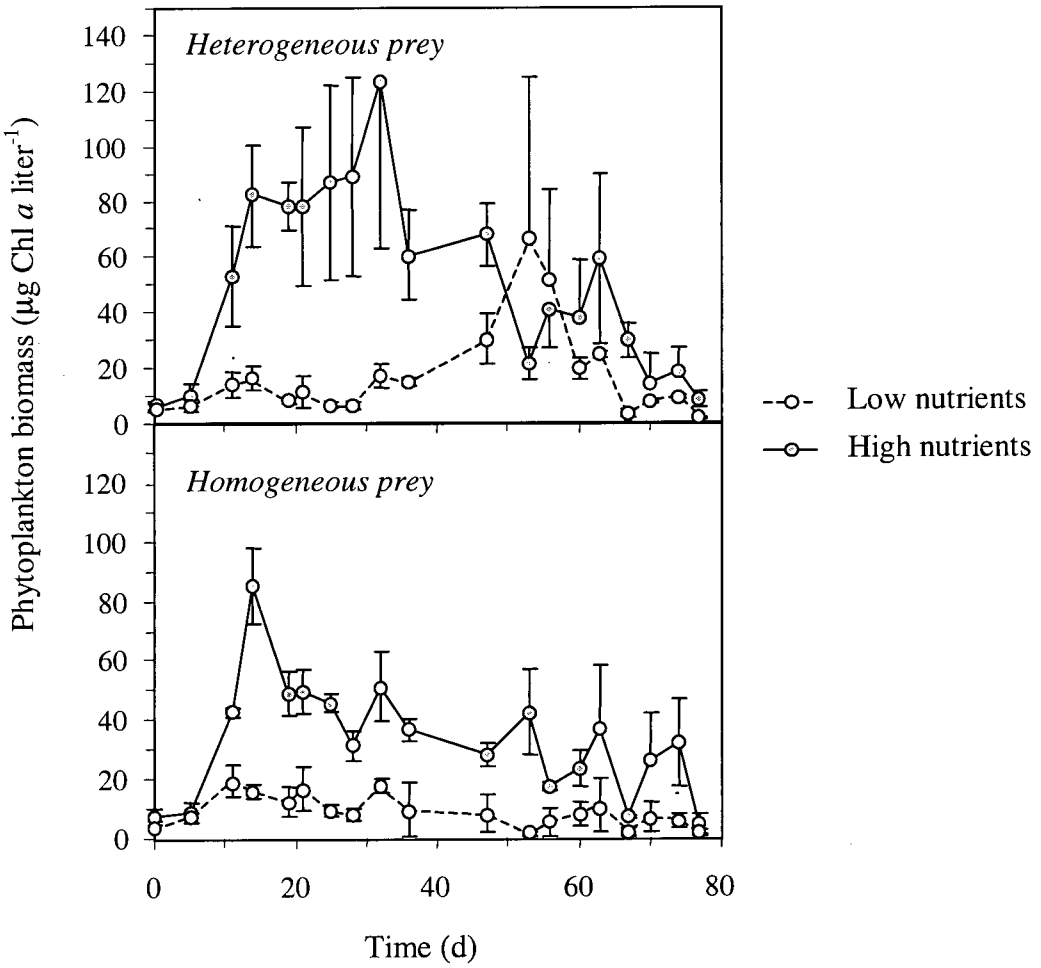
Heterogeneous prey
Homogeneous prey
Phytoplankton biomass (µg Chl a liter-1)
Time (d)
Low nutrients
High nutrients
0
20
40
60
80
100
120
140

Figure 2.2

Figure 2.3: Grand mean of the phytoplankton biomass (±SE) averaged over the course of the experiment in the two types of phytoplankton community (*Homogeneous* and *Heterogeneous prey*) and under the two nutrient regimes (*High* and *Low nutrients*). The lines connecting the columns represent pairwise comparisons between treatments using the Tukey test on log-transformed data (* $P < 0.05$). Non-significant comparisons are not indicated.

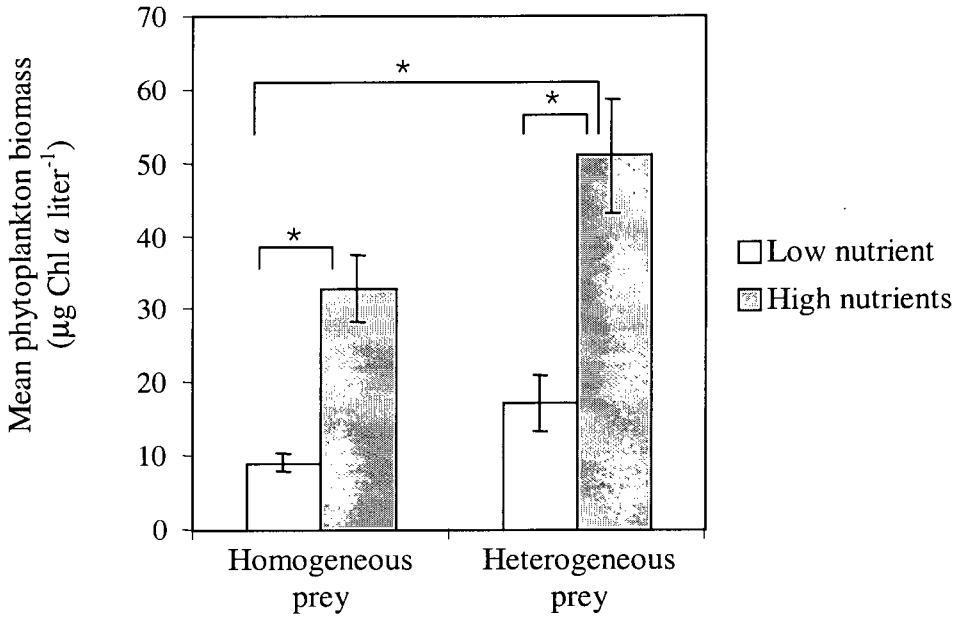
Mean phytoplankton biomass
(µg Chl a liter-1)
70
60
50
40
30
20
10
0
*
*
*
Homogeneous prey
Heterogeneous prey
Low nutrient
High nutrients

Figure 2.3

Figure 2.4: Mean (±SE) zooplankton biomass on a single sampling date near the conclusion of the experiment (20 September 2000) in the two types of phytoplankton community (*Homogeneous* and *Heterogeneous prey*) and under the two nutrient regimes (*High* and *Low nutrients*). The lines connecting the columns represent pairwise comparisons between treatments using the Tukey test on log-transformed data (* $P < 0.05$). Non-significant comparisons are not indicated.

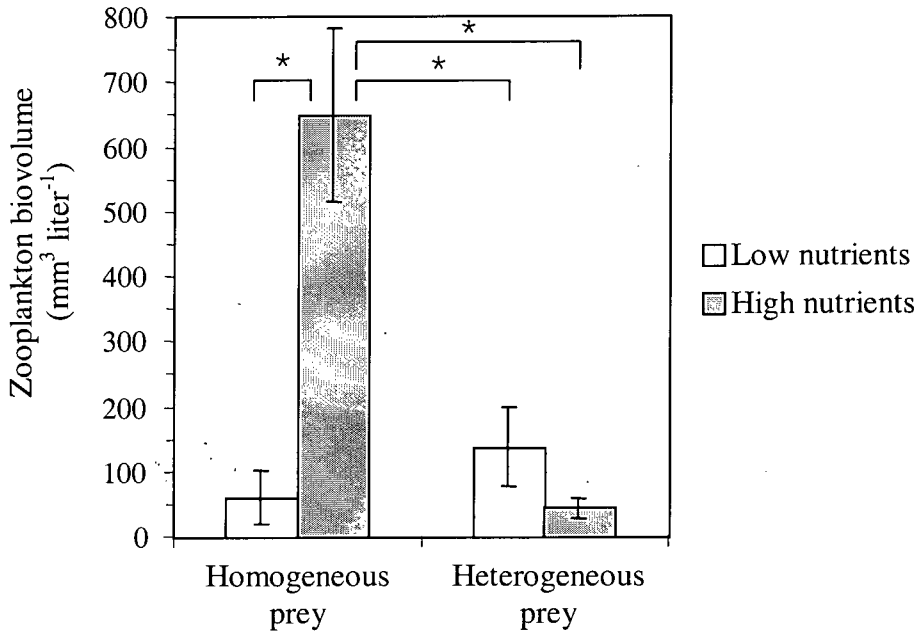
800
700
600
500
400
300
200
100
0
Zooplankton biovolume
(mm3 liter-1)
*
*
*
Homogeneous
prey
Heterogeneous
prey
Low nutrients
High nutrients

Figure 2.4

Figure 2.5: Mean (±SE) phytoplankton biomass in enclosures to which zooplanktivorous fish have (*3 trophic levels*) or have not (*2 trophic levels*) been added for the two types of phytoplankton community (*Homogeneous* and *Heterogeneous prey*). Negative values on the x-axis are data from before the start of the experiment.

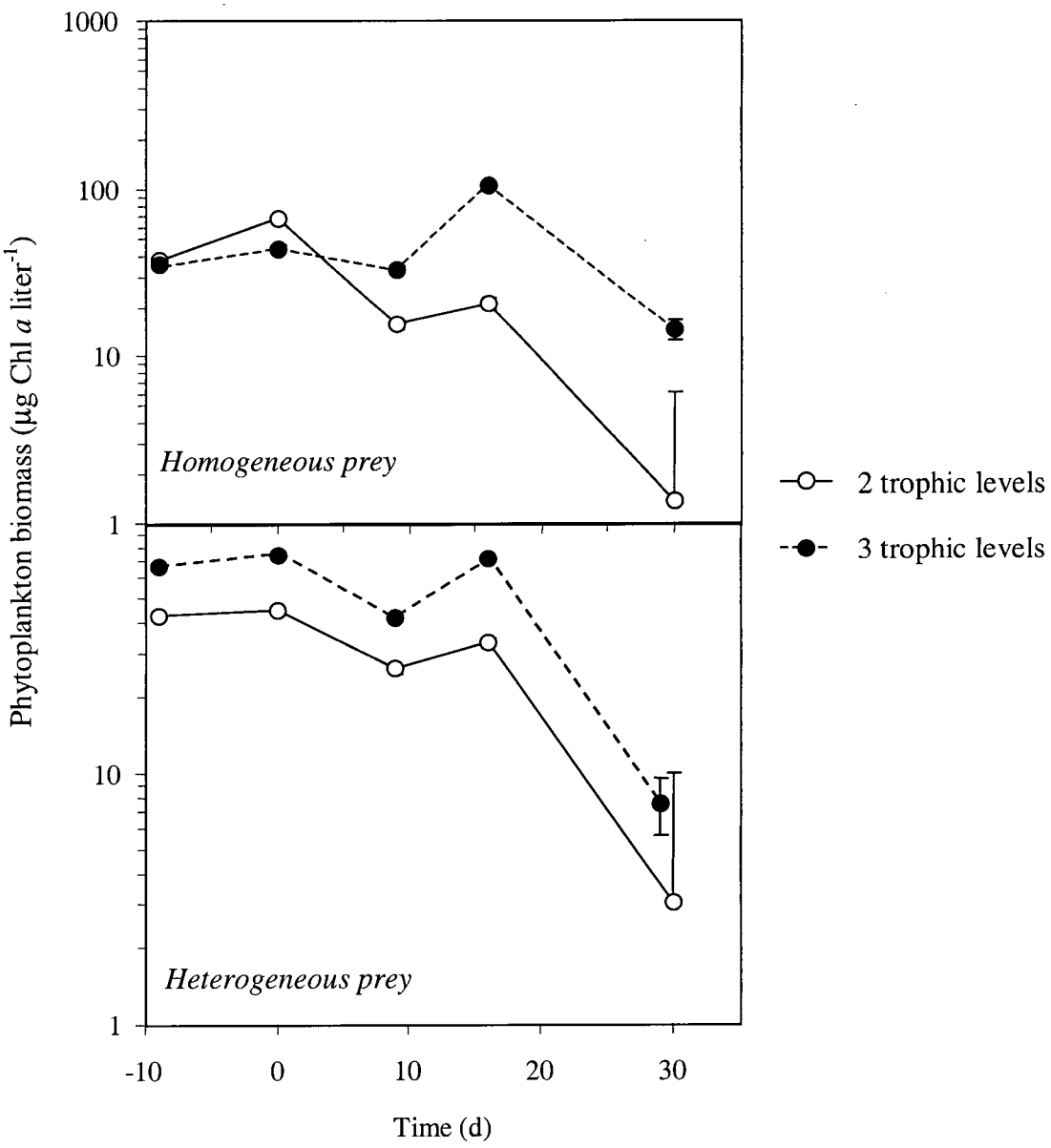
1000
100
10
1
Phytoplankton biomass (µg Chl a liter-1)
Homogeneous prey
Heterogeneous prey
10
1
-10
0
10
20
30
Time (d)
2 trophic levels
3 trophic levels

Figure 2.5

Figure 2.6: Mean (±SE) effect of fish on phytoplankton biomass in *Homogeneous* and *Heterogeneous prey* enclosures. Effect sizes are calculated by dividing the phytoplankton biomass in the *3 trophic level* treatments with the average value of the control (*2 trophic levels*) for the same date. Negative values on the y-axis are data from before the start of the experiment. Pairwise comparisons were performed at each sampling date using the Tukey test on log-transformed data (* $P < 0.05$).

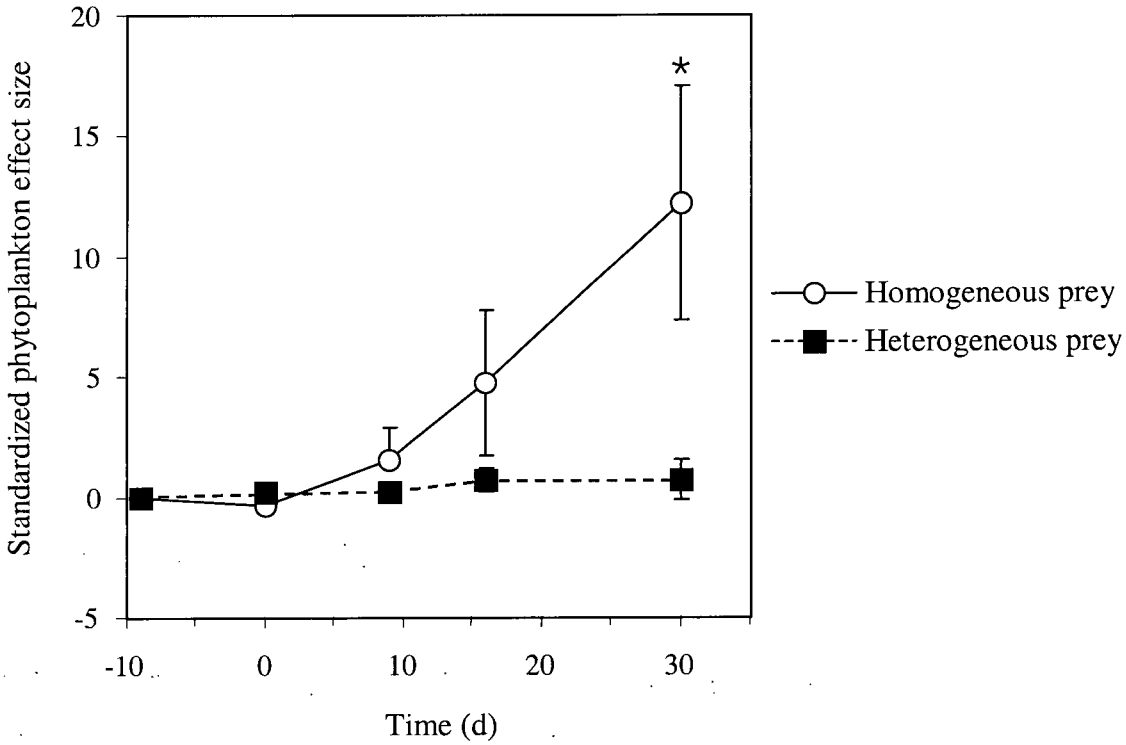
20
15
10
5
0
-5
-10
0
10
20
30
*
Standardized phytoplankton effect size
Time (d)
Homogeneous prey
Heterogeneous prey

Figure 2.6

CHAPTER III

Long live the trophic cascade

3.1 INTRODUCTION

Although the effect of predators on their prey has been well documented, the importance of the indirect effect of the top predator in determining the biomass of lower trophic levels via their direct effects on their prey remains controversial (Carpenter and Kitchell 1992, DeMelo et al. 1992, Schmitz et al. 2000, Halaj and Wise 2001). This indirect effect of the top trophic level on lower trophic levels is called the trophic cascade (Carpenter et al. 1985). There has been considerable interest in trophic cascades over the last two decades, particularly in freshwater systems (Persson 1999). The interest has arisen both from the apparent generality of the response of freshwater communities to adding or deleting the top predator (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 in aquatic ecosystems is most often tested by manipulating the top trophic level, usually zooplanktivorous fish. Trophic cascades are implicated if the elimination of zooplanktivorous fish results in increased zooplankton biomass and decreased phytoplankton biomass. A meta-analysis of top-predator addition experiments in aquatic systems has shown that a great majority of such studies conform to the predictions of the trophic cascade hypothesis (Brett and Goldman 1996). Despite that success, this meta-analysis showed a great deal of variability in the strength of the trophic cascade, that is, in the degree to which the top-predator (zooplanktivorous fish) affects herbivore (zooplankton) and primary producer (phytoplankton) 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). Although there have been some experimental results that support this view (Leibold and Wilbur 1992, Balciünas and Lawler 1995), the hypothesis was rejected by a recent meta-analysis of 11 independent experiments in freshwater enclosures in which both the presence of a third trophic level and the concentration of nutrients were manipulated (Brett and Goldman 1997). The meta-analysis showed that both nutrients and predators had a significant effect on the response of primary producer to these manipulations, but that there was no significant interaction between the two.

Several other factors, especially spatial heterogeneity (Scheffer 1998), and food web heterogeneity, such as the prevalence of omnivory (Strong 1992, Diehl 1995), interference among predators (McCann et al. 1998) and heterogeneity in prey edibility (Leibold 1989), 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.

A more troubling suggestion is that the strength of trophic cascades cannot be predicted because of inadequacies in the methodology. Replicated trophic cascade experiments typically run over very short time scales (one summer or less) and therefore last for only a fraction of a single generation of the top predator, which is insufficient to estimate the eventual outcome of the manipulation (Yodzis 1988). The consistent top-down effects that occur with the addition of a trophic level (Brett and Goldman 1996)

might disappear once top-predator density decreases as a result of declining prey density or because of delayed compensation by species that are adapted to avoid predators. Unreplicated whole-lake experiments typically endure for much longer than enclosure and pond experiments, but qualitative reviews of whole-lake experiments have suggested that the initial strong effect of removing or adding a top predator can decline in subsequent years (Shapiro 1990, McQueen 1998). It is therefore unclear whether the strong trophic cascades often observed in aquatic systems are weakened or even persist over relevant time scales.

There is also debate as to whether the enclosures and mesocosms commonly used in such experiments are appropriate models of whole lakes. While it is relatively easy to obtain the necessary replicates in enclosure and mesocosm studies, these systems do not imitate many of the processes that may be important determinants of community dynamics in lakes (Bloesch et al. 1988, Frost et al. 1988, Carpenter 1996). Conversely, the interpretation of unreplicated perturbation experiments, such as whole-lake studies, remains controversial (Stewart-Oates et al. 1992). Many of the conclusions regarding trophic cascades are derived from enclosure and mesocosm studies, but there has been little attempt to investigate whether these results are comparable to those of whole-lake manipulations. Although some of the large-scale processes that occur in lakes but not in mesocosms, such as benthic-pelagic coupling and long range biotic nutrient transport, have been shown to affect lake communities, no one has yet shown how they affect the strength of trophic cascades. While ecologists continue to debate whether large spatial scale is more important than replicability of results, the minimum spatial scale necessary to approximate whole-lakes remains unknown.

This study presents experimental and comparative data to address these concerns. I summarize the results of a 4-year (4 top-predator generations) replicated trophic cascade experiment. This experiment was more than 18 times longer than the average duration of replicated trophic cascade experiments, and almost twice as long as the longest published experiment. It is the only replicated experiment in freshwater of which I am aware that satisfies the requirement of Yodzis (1988) that experiments last for at least 2 generations of the top predator. The experiment was conducted in ponds, which are a compromise between lakes and mesocosms. The purpose of the experiment was to test two predictions of trophic cascade theory. First, that the strength of trophic cascades is undiminished over prolonged periods. Second, that the magnitude of the effect of fish on zooplankton predicted the magnitude of their indirect effect on phytoplankton. I furthermore perform a quantitative literature analysis to compare my results to those of other trophic cascade studies and to investigate whether the preceding hypotheses hold for trophic cascade experiments in general. The data from the literature allowed me to test the additional hypothesis that trophic cascade experiments in different types of study system (lakes, ponds, mesocosms, enclosures) produce quantitatively different results when the topmost trophic level is manipulated.

3.2 METHODS

Study site and Experimental Design

The study was conducted in 4 experimental ponds at the University of British Columbia, Canada from 6 July 1993 to 21 August 1997. The ponds are 23×23 m^2, 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, each twice replicated. Zooplanktivorous fish (see below) were added to 2 of the 4 ponds, and the 2 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 during 1992 using the same species as that used in the present study. Fish had been removed from this pond 4 months prior to the beginning of this study using minnow traps.

Fish

Fish were introduced to 2 of the ponds during May 1993. I used a Limnetic species of the threespine stickleback (*Gasterosteus* sp.), one of several populations endemic to 5 lakes (formerly 6) 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 (usually 1 year). Furthermore, 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 1000 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 d 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, I 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. A total of 150 fish were removed from the ponds over the course of the experiment to enumerate gut contents.

Zooplankton

Zooplankton were sampled periodically during the summer and early fall by pumping 15 to 75 L of water through 62 μm 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

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 μm 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.

Literature Analysis

I searched the literature for experiments for experiments in which zooplanktivorous fish were present or absent. I 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 ponds, enclosures (bags and lake enclosures and exclosures), mesocosms (cattle tanks, plastic pools, etc.), and lakes. To distinguish lake from pond studies, a pond study was defined as one in which there were replicated man-made water bodies of similar size and shape each with an area <1 ha, and which contained an evident benthic and limnetic invertebrate community. Unreplicated studies of lakes <1 ha were excluded from the analysis. Effect sizes were calculated by comparing the treatments with and without zooplanktivorous fish in replicated studies, and by comparing high and low zooplanktivore abundance in whole-lake studies unless data from appropriate control lakes were available. I used some whole-lake manipulations that reduced planktivore abundance by adding a piscivorous fish, but only when this method was accompanied by some other method 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 to 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.

Statistical analyses

Repeated measures analysis of variance (ANOVAR) was used to estimate treatment effects over the course of my experiment using SYSTAT 5.05. Data were log-transformed prior to statistical analyses to homogenize the variances. I 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. For comparisons of the zooplankton and phytoplankton effect sizes between system types (mesocosm, enclosure, pond, lake) and duration categories (*Summer*, *1 year*, *>1 year*) I used analysis of variance (ANOVA) on log-transformed data to estimate differences among categories. I also tested for differences in the coefficient of variation among the duration categories and types of system (Zar 1996).

3.3 RESULTS

Fish

Fish numbers fluctuated dramatically both between and within years (Table 3.1). Observations from wild populations (D. Schluter, personal communication) indicate that this may have been largely due to within-year differences in trappability. Unfortunately, there are insufficient data to test this hypothesis.

The gut contents of the fish were also highly variable. No single species consistently dominated stickleback guts. 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 longirostrus*, amphipods, *Diaphanosoma*, and ostracods were all numerically important during different years or in different ponds, but were never consistently important.

Zooplankton

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 4 sampling dates at the outset of the experiment in 1993 (Figure 3.1). There were both a significant Time effect ($F_{10,20}$ = 7.2, P < 0.0001) and a significant Treatment × 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 dominated by smaller zooplankton species, especially *Bosmina* and *Chydorus*. The invertebrate predator *Chaoborus* was present at low densities at the outset of the experiment in both control and treatment ponds (Figure 3.2), but became more abundant in control ponds after the first two years of the experiment (ANOVAR: $F_{1,2} = 52.4$, $P = 0.019$).

Phytoplankton

There was a higher total biovolume of phytoplankton in ponds with fish present compared to ponds without fish (ANOVAR; $F_{1,2} = 69.3$, $P = 0.014$) (Figure 3.3). There was no significant time effect ($F_{12,24} = 1.0$, ns), nor was there any interaction between time and treatment effects ($F_{12,24} = 0.6$, ns). Phytoplankton were divided in 2 categories based on their edibility to common zooplankton. Phytoplankton greater than approximately 30-60 μm 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, 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 μm 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 μm diameter) in the control ponds (Figure 3.4; ANOVAR: $F_{1,2}$ = 85.65, $P = 0.011$).

Effect of experiment duration

The results from my experiment indicate that the zooplankton were consistently greater in ponds without fish for all data points subsequent to the first year of the study (Figure 3.1). 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 in the total phytoplankton biovolume during the first year of the experiment (ANOVAR: $F_{1,2}$ = 0.11, ns). The phytoplankton biomass was considerably higher in the pond with fish on all sampling dates except during the 4th year of the study (1996) when there was little difference in the phytoplankton biomass between the fish and control ponds. 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 (Figure 3.3).

To assess whether the strength of trophic cascades was generally affected by experiment duration, I divided published studies into 3 duration categories (*Summer, 1 year, >1 year*) (Figure 3.5). Effect sizes (the magnitude of change resulting from the addition of fish) were calculated for each independent experiment (Table 3.2). There was no significant difference among categories in the log-transformed phytoplankton effect sizes (ANOVA: $F_{2,88}$= 1.1, ns). There was, however, a significant difference among the log-transformed zooplankton effect sizes (ANOVA: $F_{2,75}$ = 4.96 , P = 0.009). Pairwise comparisons indicated that this difference was due to significantly smaller zooplankton

effect in the *>1 year* category than the *Summer* category (Tukey test: $q_{75,3}$ = 3.81, P = 0.024) and the *1 year* category (Tukey test: $q_{75,3}$ = 3.96, P = 0.018) categories. There was no difference between the *Summer* and *1 year* effect sizes (Tukey test: $q_{75,3}$ = 1.14, P = 0.701).

I also tested to see whether the variability (coefficient of variation) of the effect sizes differed among the duration categories. I found that the coefficient of variation of the phytoplankton effect sizes was significantly higher in experiments that lasted for one summer than for experiments that lasted for longer than a year (t_∞= 2.24, p = 0.025) but that there was no significant differences for any of the other pairwise comparisons. The coefficient of variation of the zooplankton effect sizes were significantly higher in the *Summer* category compared to *<1 year* (t_∞= 2.31, p = 0.022) and *>1 year* (t_∞= 2.21, p = 0.028) experiments, and was also higher for *<1 year* compared to *>1 year* experiments (t_∞= 4.24, p < 0.0005).

Whole-lakes were the only study system that had sufficient data from all 3 duration categories to warrant statistical tests that could control for the system of study. There was a significant difference in the phytoplankton effect sizes among the 3 duration categories when only the whole-lake data were used (Table 3.2; $F_{2,26}$ = 7.5, P = 0.003) owing to a significantly larger phytoplankton effect in the *Summer* category compared to the *<1 year* category (Tukey test: $q_{3,26}$ = 4.03, P = 0.022) and *>1 year* studies (Tukey test: $q_{3,26}$ = 5.45, P = 0.002). There was no significant difference among the 3 categories for the zooplankton effect sizes ($F_{2,22}$ = 1.5, ns), although there were only 2 data points in the *Summer* category.

Trophic coupling

Tight coupling between trophic levels is implied if the magnitude of the effect of a disturbance on one trophic level is transmitted at the same magnitude to the trophic level above or below. In my long-term experiment, the addition of zooplanktivorous fish resulted in an average 18.24-fold decrease in zooplankton, and a 5.69-fold increase in phytoplankton. However, there was no difference between these effect sizes (t_{22} = 1.22, P = 0.12). In my across-studies comparison, the addition of zooplanktivorous fish in general resulted in a 2.55-fold decrease in zooplankton and a 2.18-fold increase in phytoplankton, but there was similarly no difference between these effect sizes (t_{167} = 0.97, ns).

Tight coupling is also implied if there is a significant relationship between zooplankton and phytoplankton effect sizes, either over time within an experiment, or across studies. Although the pattern of effect sizes was somewhat similar in my experiment between zooplankton and phytoplankton (Figure 3.6), there was no relationship between zooplankton and phytoplankton effect sizes for the dates where data were available for both zooplankton and phytoplankton ($F_{1,7}$ = 0.66, ns, R^2 = 0.09). The absence of a relationship was due to a more rapid response of the zooplankton to zooplanktivore additions at the outset of the experiment, and a dip in the phytoplankton effect size during 1996 that did not occur in the zooplankton. In my across-studies comparison, I similarly found that there was no relationship between zooplankton and phytoplankton effect sizes (Figure 3.7; $F_{1,76}$ = 0.83, ns).

When data points from particular system types (ponds, mesocosms, enclosures, whole-lakes) were analyzed separately (Table 3.3), there was a significant relationship between zooplankton and phytoplankton effect size for pond studies ($F_{1,9}$ = 10.9, P =

0.009, $R^2 = 0.55$), but not for mesocosms, enclosures or whole-lakes (Figure 3.7). There was no difference in the effect of fish on phytoplankton biomass among studies that were conducted in different system types ($F_{3,87} = 0.4$, ns), but there was a significant difference among zooplankton effects ($F_{3,74} = 7.0$, $P = 0.0003$). This was due to a significantly larger zooplankton effect size in mesocosm studies compared to enclosure (Tukey test: $q_{75,4} = 4.49$, $P = 0.012$) and whole-lake (Tukey test: $q_{75,4} = 5.44$, $P = 0.002$) studies (Table 3.3). The zooplankton effect was also significantly higher in ponds compared to lakes (Tukey test: $q_{75,4} = 3.90$, $P = 0.016$) but was heavily influenced by 3 outliers with very high zooplankton effects in ponds (Figure 3.7).

The variability (coefficient of variation) among studies in the zooplankton effect sizes was significantly lower in lake studies compared to pond ($t_\infty = 3.67$, $p = 0.008$) and enclosure ($t_\infty = 2.58$, $p = 0.01$) studies, and was also significantly lower in mesocosm compared to ponds ($t_\infty = 2.08$, $p = 0.039$). No other comparison was significant. There was no significant difference between any pair of system types in the coefficients of variation of phytoplankton effect size.

3.4 Discussion

Several authors have argued that trophic cascades are unlikely in complex food webs, where inedible species, omnivores, and interference among competing predator species are likely to preclude the propagation of top-down signals (Strong 1992, Morin and Lawler 1995). The results of my across-studies comparison, supported by other similar meta-analyses (Brett and Goldman 1996, Leibold et al. 1997) indicate that the

trophic cascade is an important and indeed ubiquitous feature of lentic freshwater systems, from small-scale enclosure and microcosm experiments to whole-lake manipulations. Previous experiments have shown, however, that a number of factors can modify the outcome of trophic cascade experiments, including spatial and temporal heterogeneity, heterogeneity in prey edibility, and self regulation of trophic levels through omnivory, intraguild predation, and territoriality (Polis et al. 2000). Given the multiplicity of these secondary factors, it is surprising that even the qualitative hypotheses of the trophic cascade are supported in the great majority of studies. Although these factors appear to be important in preventing trophic cascades in many terrestrial systems (Schmitz et al. 2000) and might play a role in some of the instances of failed trophic cascades in freshwater systems (DeMelo et al. 1992, Badgery et al. 1994), my across-studies comparison shows that they appear to be insufficient to block trophic cascades in the great majority of cases in freshwater.

Compensation within trophic levels is often cited as being responsible for the absence of a trophic cascade. Compensation occurs when higher levels of predation do not result in reduced biomass of the prey, but instead in an increased abundance of less edible prey. The long-term experiment provides some of the clearest documented evidence for compensation by large phytoplankton when zooplankton are abundant, but this compensation still fails to prevent a net decline in the phytoplankton biomass in the absence of zooplanktivorous fish. Similarly, compensation by the invertebrate zooplanktivore *Chaoborus* in the absence of zooplanktivorous fish has the potential to stabilize zooplankton densities and therefore also phytoplankton densities. My long-term

experiment shows that even clear compensation by *Chaoborus* is insufficient to preclude the trophic cascade.

However, my across-studies comparison indicates that zooplanktivorous fish can have a wide range of effects on zooplankton without subsequent effects of similar magnitude on phytoplankton (Figure 3.7). Therefore, although several authors have presented clear evidence that zooplankton refuges (e.g. macrophytes) play a key role in preventing declines in zooplankton biomass and therefore increases in phytoplankton biomass (Scheffer 1998), my comparative data show that the zooplankton biomass alone is a poor predictor of phytoplankton biomass. The community composition of the zooplankton and phytoplankton rather than only biomass may therefore be more important determinants of their response to manipulations of higher trophic levels. The absence of a relationship between zooplankton and phytoplankton effect sizes unfortunately makes it difficult to predict the outcome of programs to control eutrophication by biomanipulation.

My experimental results 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 I am 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). The great majority of previous reports of replicated mesocosm, enclosure, and pond

experiments have lasted for considerably less than a single generation of the top predator. Although the duration of whole lake manipulations is typically longer than for whole-lake manipulations, few have run for the amount of time required to estimate the eventual outcome of the manipulation (Carpenter 1988, McQueen 1998).

I hypothesised that the strength of the trophic cascade would decline following the original reduction of zooplankton, either because of delayed compensation by inedible phytoplankton and zooplankton or because of declines in zooplanktivore densities as they adjust to the lowered zooplankton biomass. The results indicate, however, that inedible phytoplankton compensate rapidly following declines in the edible phytoplankton, making it unlikely that there would be any long-term declines in the strength of the trophic cascade. The resolution of my estimates of stickleback densities are probably marred by intra-annual variation in trappability, which makes it difficult to see how they adjust to the initial declines in the zooplankton standing crop. I therefore conclude from my experimental results that there is no evidence for a decline in the strength of the trophic cascade over prolonged periods.

My analysis of published reports is in general agreement with the results of the long-term experiment. The results indicate that the great majority of studies also show a decrease in the zooplankton and an increase in the phytoplankton biomass, and that these results do not diminish over longer time scales. Rather, my analysis shows that trophic cascades are not only ubiquitous, but are also persistent. 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 d) can considerably decrease the variability of the phytoplankton response to manipulations of higher trophic levels.

The comparisons are unfortunately confounded by differences between the type of system 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 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 my literature analysis also demonstrate that there are systematic differences in both the mean and variance of the results of trophic cascades that depend on the type of system in which the study is conducted. Although such differences between small scale and whole-lake manipulations have been suggested previously, especially by proponents of whole-lake manipulations (Carpenter 1996), there has been little effort to verify the accuracy of this assumption. The criteria necessary for a successful biomanipulation have, of necessity, relied on comparative data. Unfortunately, this makes it difficult to understand the variables that actually determine the strength of the trophic cascade because many of the morphometric and biological characteristics of lakes covary. For example, because of recent biomanipulation failures in some large lakes, it has been suggested that strong trophic cascades are unusual in large deep lakes, perhaps because of compensation by inedible algal species and by invertebrate zooplanktivores (McQueen 1998). The results suggest that researchers should be cautious in extrapolating the results of small-scale studies to larger systems.

Table 3.1

Fish dynamics in the two ponds to which fish were added. *Density* estimates are the number of fish caught in minnow traps over 24 h. A mark recapture experiment in 1994 indicated that on average 76.3% of the population was caught in 24 h. Mean population sizes (mean number of fish per pond) were therefore estimated as the mean *Density* multiplied by 1.237. The first row of data is the number of fish introduced into the ponds.

Date	Density in Pond 1 (fish caught 24 h^{-1})	Density in Pond 2 (fish caught 24 h^{-1})	Mean population size (fish $pond^{-1}$)
6 July 1993	..	..	925
26 March 1994	182	164	244.9
23 June 1994	102	253	93.4
6 June 1995	768	793	965.5
11 April 1996	625	486	443.5
1 April 1997	486	629	554.2

Table 3.2

Among-study mean effect of fish on zooplankton (control/fish) and phytoplankton (fish/control) biomass for experiments that lasted for a single summer, for 4-12 months, and for longer than one year. Means, standard errors (SE), and coefficients of variation (CV) are calculated from the untransformed data. Samples sizes (n) of phytoplankton and zooplankton effect sizes are not equal for a given duration category because some studies reported phytoplankton but not zooplankton biomass.

		Phytoplankton effect size				Zooplankton effect size			
	Duration	n	Mean	SE	CV	n	Mean	SE	CV
All data	Summer	52	3.41	0.57	1.21	43	7.03	1.76	1.64
	4-12 months	16	3.41	0.78	0.91	14	56.98	47.14	3.15
	>1 year	23	2.18	0.25	0.54	21	1.25	1.59	0.26
Whole-lakes	Summer	4	10.98	5.06	1.08	2	2.81	2.20	0.90
	4-12 months	4	2.17	0.54	2.00	4	3.15	1.30	1.21
	>1 year	21	2.13	0.27	1.74	19	1.56	0.27	1.33

Table 3.3

Among-study mean effect of fish on zooplankton (control/fish) and phytoplankton (fish/control) in enclosure, mesocosm, pond, and whole-lake experiments. Means, standard errors (SE), and coefficients of variation (CV) are calculated from the untransformed data.

		Phytoplankton effect size			Zooplankton effect size		
	n	Mean	SE	CV	Mean	SE	CV
Enclosure	25	2.68	0.43	0.92	3.32	1.27	1.91
Mesocosm	17	3.36	0.84	1.03	10.77	3.40	1.30
Pond	11	3.26	0.72	0.77	73.23	59.59	2.70
Lake	25	3.36	0.87	1.39	1.91	0.33	0.86

Figure 3.1: Mean (± SE) total zooplankton biomass in control ponds and ponds with fish. Error bars are asymmetric on a logarithmic scale. The shaded areas are fall sampling dates (1 September to 1 November).

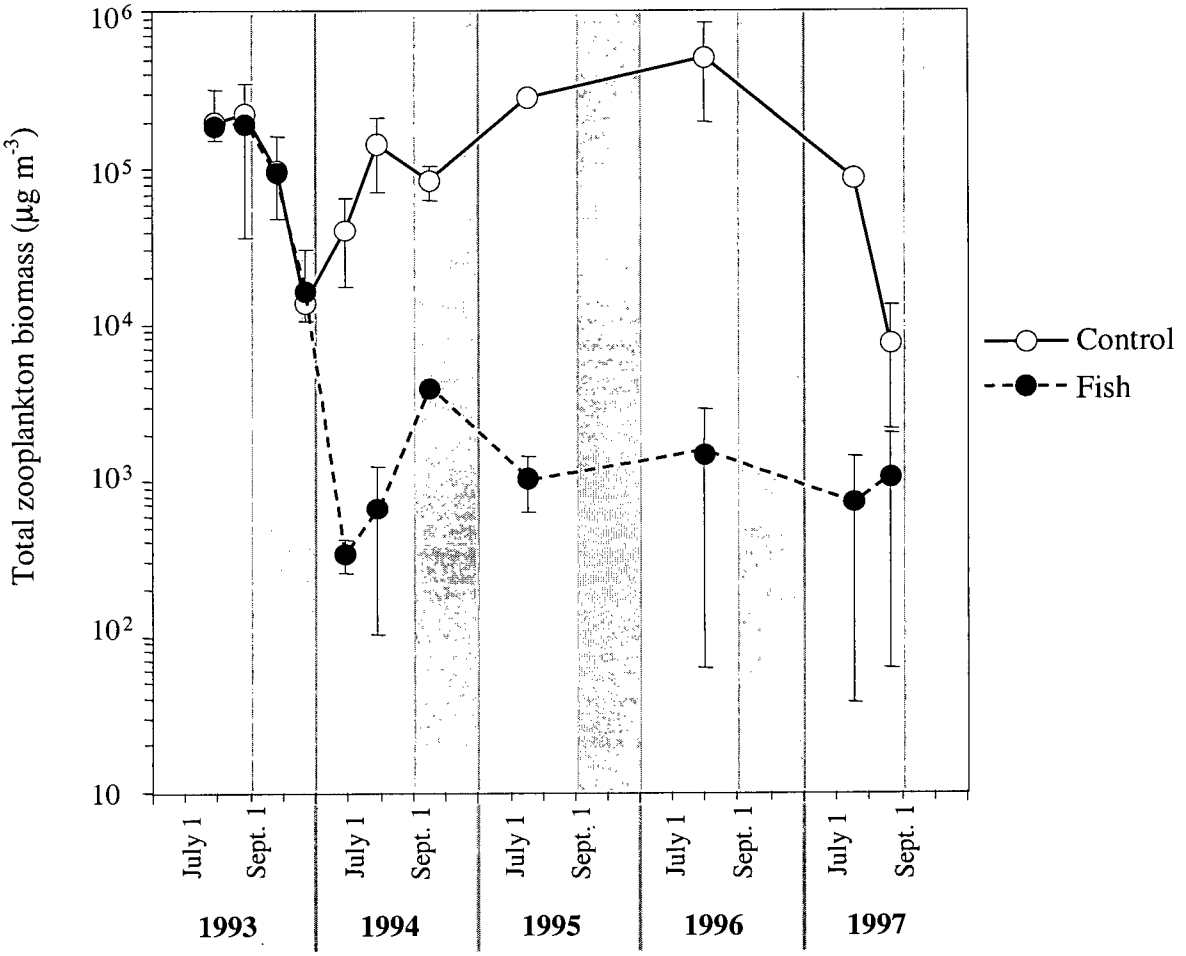
Total zooplankton biomass (µg m-3)
10^6
10^5
10^4
10^3
10^2
10
July 1
Sept. 1
1993
1994
1995
1996
1997
Control
Fish

Figure 3.1

Figure 3.2: Mean (± SE) abundance of the invertebrate zooplanktivore *Chaoborus* in control ponds and ponds with fish. Error bars are asymmetric on a logarithmic scale. The shaded areas are fall sampling dates (1 September to 1 November).

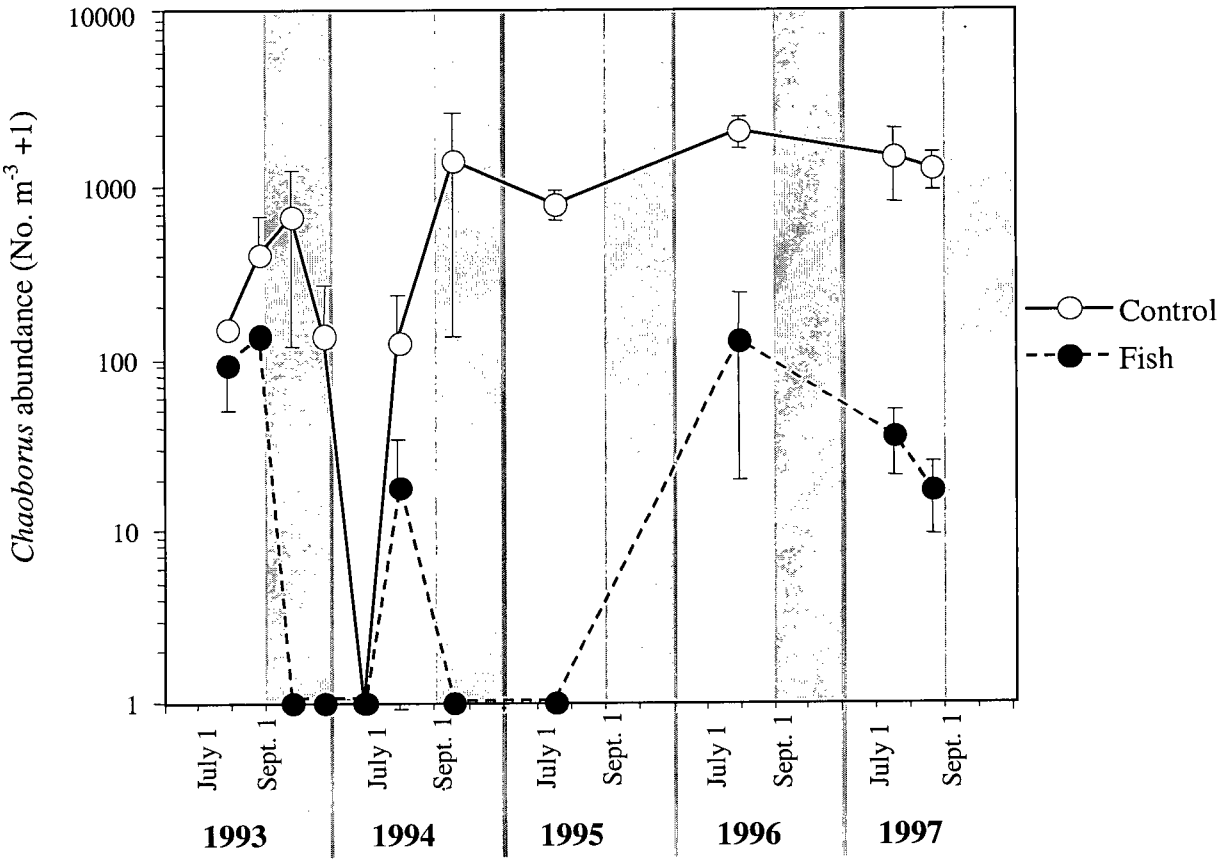
10000
1000
100
10
1
Chaoborus abundance (No. m^{-3} +1)
July 1
Sept. 1
1993
1994
1995
1996
1997
Control
Fish

Figure 3.2

Figure 3.3: Mean (± SE) phytoplankton biovolume in control ponds and ponds with fish. Error bars are asymmetric on a logarithmic scale. The shaded areas are fall sampling dates (1 September to 1 November).

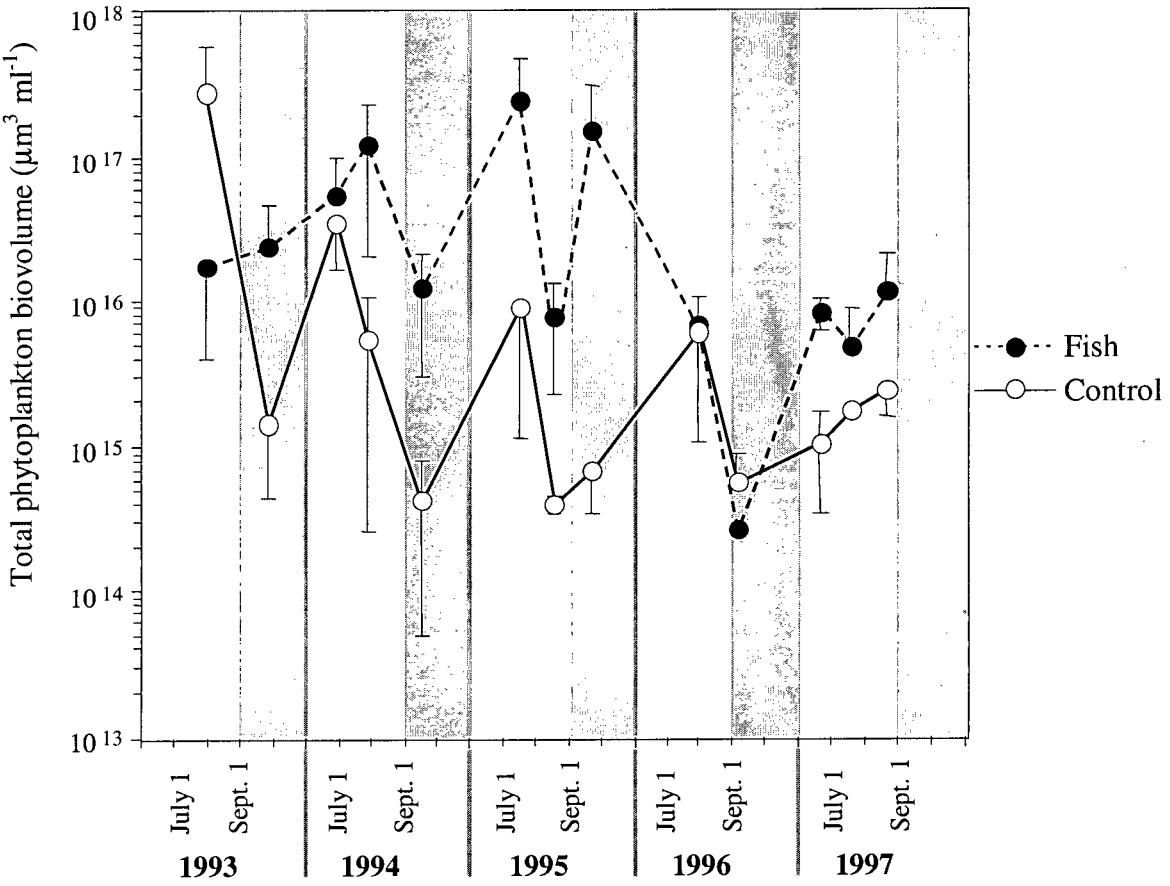
Total phytoplankton biovolume (µm³ ml⁻¹)
10 18
10 17
10 16
10 15
10 14
10 13
July 1
Sept. 1
1993
1994
1995
1996
1997
Fish
Control

Figure 3.3

Figure 3.4: Mean (± SE) abundance of inedible phytoplankton in control ponds and ponds with fish. Error bars are asymmetric on a logarithmic scale. The shaded areas are fall sampling dates (1 September to 1 November).

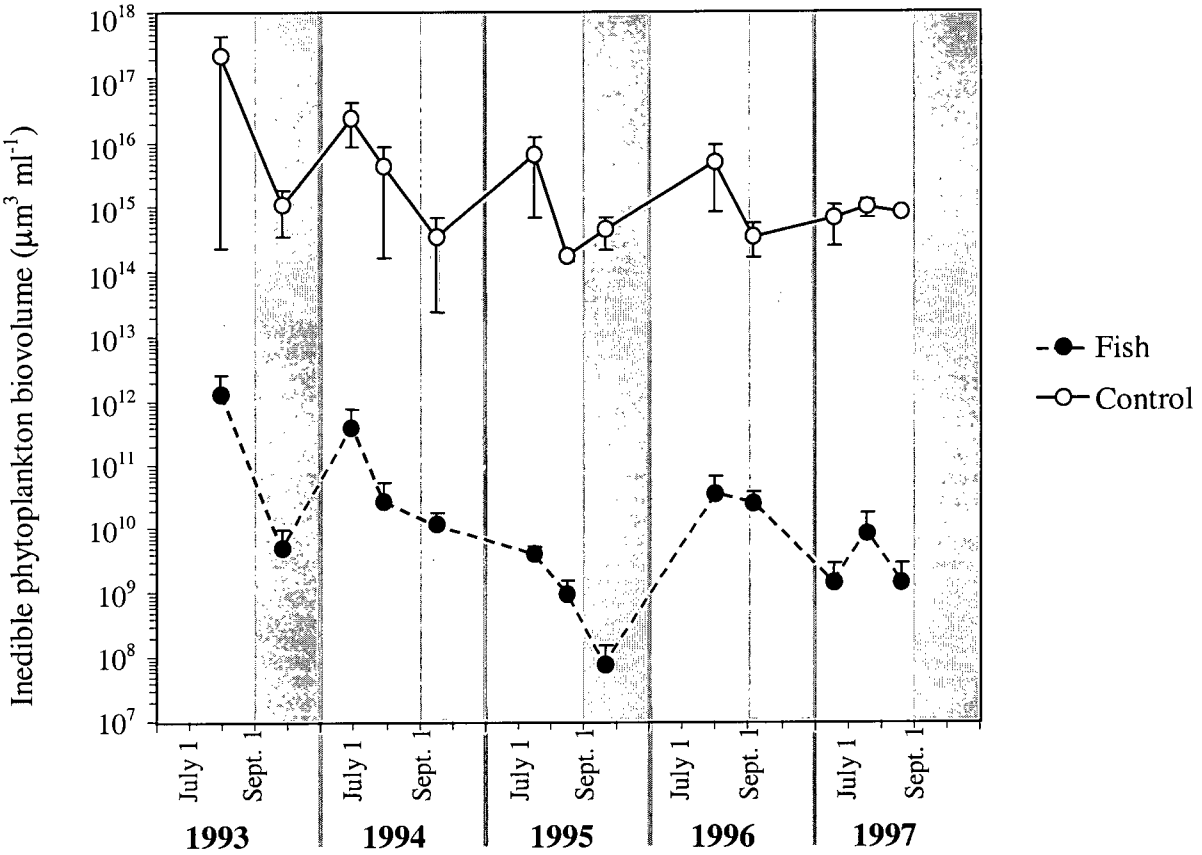
Inedible phytoplankton biovolume (μm³ ml⁻¹)
10¹⁸
10¹⁷
10¹⁶
10¹⁵
10¹⁴
10¹³
10¹²
10¹¹
10¹⁰
10⁹
10⁸
10⁷
July 1
Sept. 1
1993
1994
1995
1996
1997
Fish
Control

Figure 3.4

Figure 3.5: The effect of fish on (A) zooplankton and (B) phytoplankton 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. References from which data were obtained are given in the Appendix.

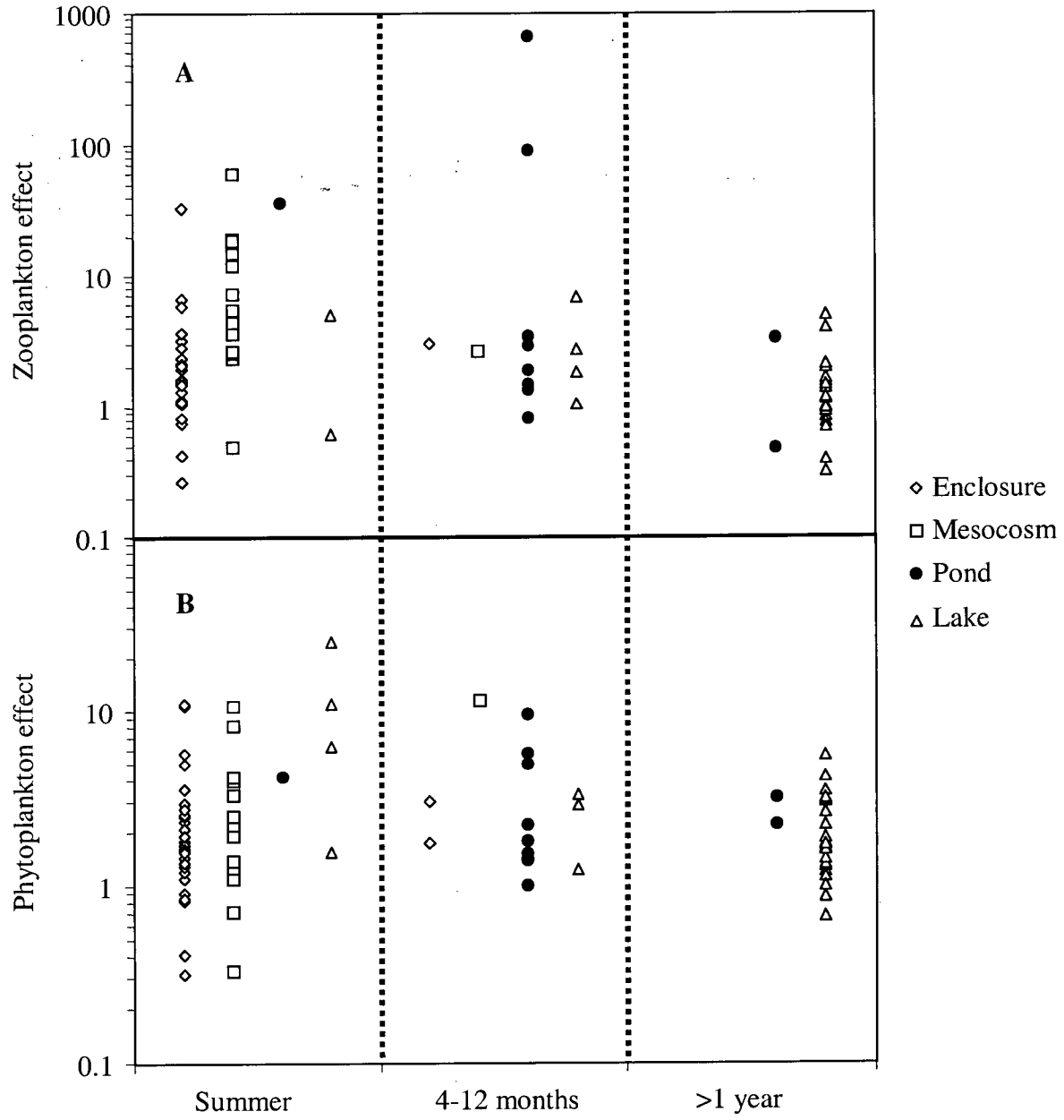
1000
100
10
1
0.1
A
B
Zooplankton effect
Phytoplankton effect
Summer
4-12 months
>1 year
Enclosure
Mesocosm
Pond
Lake

Figure 3.5

Figure 3.6: Effect of fish on the biomass of phytoplankton (fish/control) and zooplankton (control/fish) over the course of the experiment. Large symbols indicate data points used to test for a relationship between zooplankton and phytoplankton effect sizes. The shaded areas are fall sampling dates (1 September to 1 November).

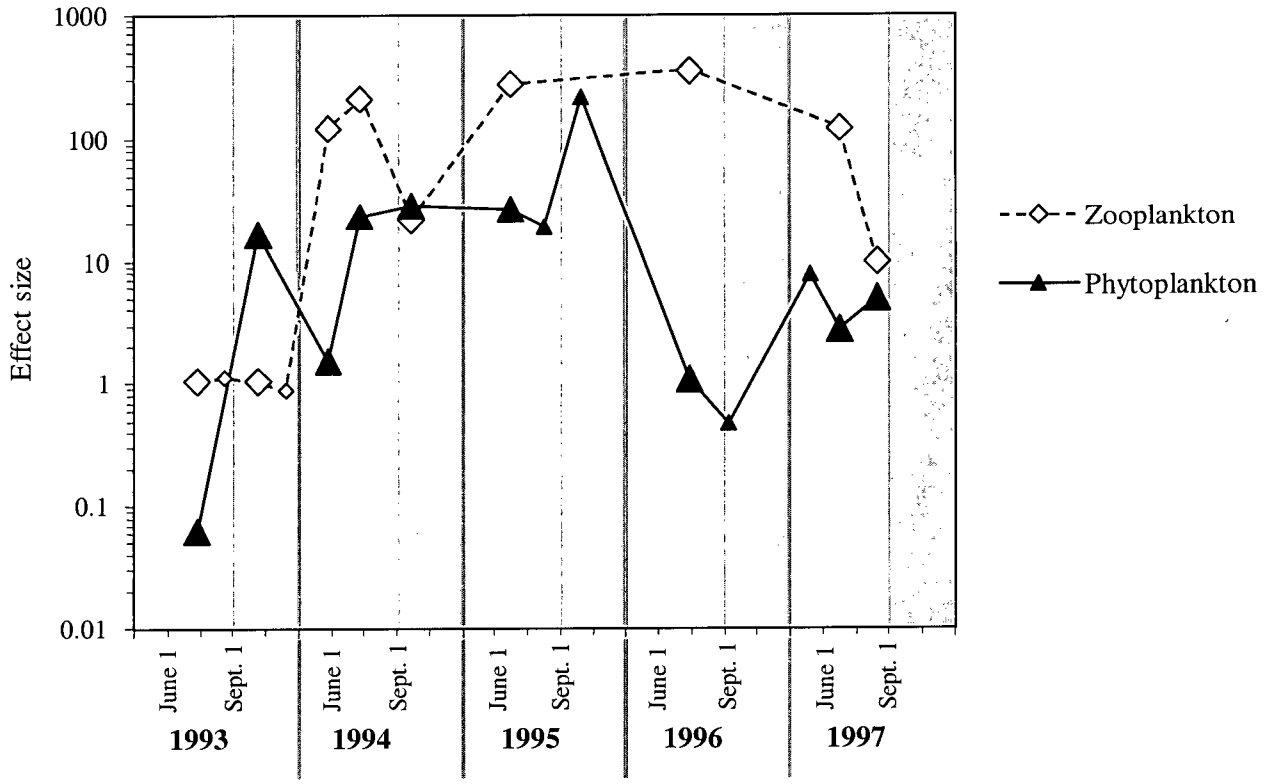
1000
100
10
1
0.1
0.01
Effect size
June 1
Sept. 1
1993
1994
1995
1996
1997
Zooplankton
Phytoplankton

Figure 3.6

Figure 3.7: 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 line (1^{st} quadrant) 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.

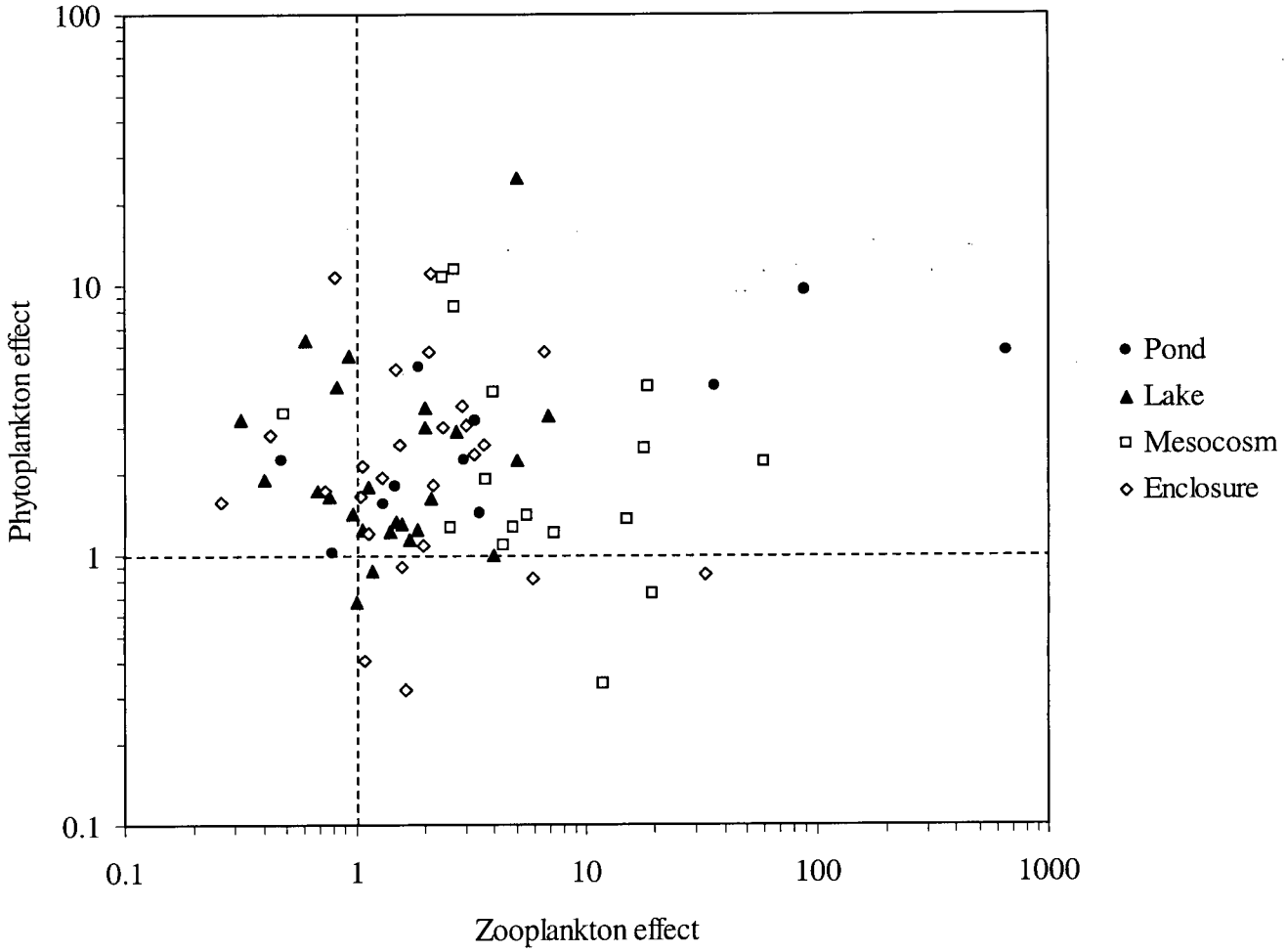
100
10
1
0.1
Phytoplankton effect
0.1
1
10
100
1000
Zooplankton effect
Pond
Lake
Mesocosm
Enclosure

Figure 3.7

CHAPTER IV

Conclusions

4.1 General conclusions

The combined results of the two experiments presented in Chapter II demonstrate the importance of prey heterogeneity in determining the balance between top-down and bottom-up regulation. I show that the presence of inedible phytoplankton can alter the response of the phytoplankton to nutrient additions and the addition of a trophic level. Theoretical (Genkai-Kato and Yamamura 1999, Huxel 1999) and experimental (Bohannan and Lenski 1999) work has further shown that not only the standing crop biomass but also the variability and stability of the biomass is affected by the presence of inedible species. Unfortunately, there are few experiments that explicitly manipulate prey edibility despite the hypothesised importance of inedible species in determining the dynamics of trophic levels. I hope my work will stimulate further efforts.

Despite the importance of inedible species, they were unable to compensate for the losses incurred by the edible phytoplankton in the long-term experiment presented in Chapter III. There was therefore little evidence for a diminution of the trophic cascade over the course of the experiment. Similarly, the across-studies comparison demonstrated that there was no strong effect of experiment duration on the strength of the trophic cascade. The decline in the strength of the trophic cascade with increasing experiment duration when the analysis is restricted to whole-lake manipulations warns that such analyses are not conclusive. The analysis demonstrates that short-term and small-scale experiments produce results that are highly variable, and consequently, difficult to extrapolate larger systems. Naturally, this conclusion also extends to the results of the experiments presented in Chapter II.

4.2 Further Work

The experiments presented in Chapter II underline the importance of understanding the dynamics of functional groups within a trophic level. Removal of other types of functional groups, such as omnivores (Diehl 1995), dominant herbivores (Persson et al. 2001) or intraguild predators (Polis and Holt 1992, Rosenheim et al. 1993, Morin 1999) has similarly proved to be a fruitful method of understanding the dynamics of trophic levels and communities. Such studies, and including the present one, demonstrate that the debate on whether the abundance of organisms is principally determined by nutrient supply or predation levels will only be resolved in the context of the food web in which the organisms of interest are embedded.

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 in whole-lake manipulations. As the results of Chapter III are among the first to show, the results of small-scale experiments often produce quantitatively different results from those of large-scale manipulations. I believe that, rather than dismissing the results of such experiments as inadequate at the spatial scale of a whole lake, it is necessary to identify the way in which trophic cascades are altered because of the small spatial alone. Such an understanding is also 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.

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APPENDIX I

List of references from which data were obtained for my analyses of published results of trophic cascade experiments (Figures 3.5 and 3.7).

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