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A Comparison of Lakes and
Lake Enclosures with Contrasting
Abundances of Planktivorous Fish

BY

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Running Head: Top-down impacts in enclosures and lakes

**A comparison of lakes and lake enclosures with contrasting abundances of
planktivorous fish**

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EXECUTIVE SUMMARY

Traditionally, it was thought that nutrients, particularly phosphorus, was solely responsible for the quantity and quality of the phytoplankton species composition in lakes. In the present investigation, nutrients (nitrogen and phosphorus) and planktivorous fish just over 1 year old were added to enclosures in a 2x2 factorial design. In this way, nutrient effects could be distinguished from "top down" effects of the fish. Results were compared to other lakes with known levels of planktivorous fish.

Increased planktivorous fish predation resulted in increased total phosphorus concentrations with a decrease in larger zooplankton and an increase in small algae. This occurred along with increased phosphate limitation (measured using turnover time) increased chlorophyll a and reduced water clarity.

These results have direct management implications. Phosphorus loading to lakes may influence chlorophyll levels but changes in community structure through changes in piscivore abundance (as in Lake Ontario) can have an overriding influence.

RÉSUMÉ EXPLICATIF

De tout temps, on a cru que les éléments nutritifs, particulièrement le phosphore, constituaient l'unique facteur qui, sur les plans quantitatif et qualitatif, influait sur la composition de la communauté phytoplanctonique dans les lacs. Au cours de cette étude, on a ajouté des éléments nutritifs (azote et phosphore) à des enceintes contenant des poissons planctonophages d'un peu plus d'un an. Un plan d'expérience factoriel 2x2 a été retenu. De cette manière, on a pu établir une distinction entre les effets des éléments nutritifs proprement dits et les effets "descendants" des poissons. On a ensuite comparé les résultats avec ceux des études effectuées dans des lacs où l'abondance des poissons planctonophages était connue.

La prédation accrue de la part des poissons planctonophages s'est traduite par une augmentation des concentrations de phosphore total, une diminution des organismes zooplanctoniques de grande taille et une augmentation du nombre de petites algues. En outre, on a observé une diminution de la concentration de phosphate (d'après le temps de renouvellement), un accroissement de la teneur en chlorophylle a et une diminution de la limpidité de l'eau.

Ces résultats ont des répercussions directes sur la gestion. Les rejets de phosphore dans les lacs peuvent influencer sur les concentrations de chlorophylle, mais les effets des changements de la structure des communautés dus aux variations de l'abondance des poissons (comme dans le lac Ontario) peuvent être davantage marqués.

Résumé. Des manipulations expérimentales avec des poissons planctonophages dans d'importantes enceintes ont produit des communautés de planctons comparables à celles observées dans des lacs où l'abondance de ces poissons variait. Le phosphore total (PT) dans la zone épilimnique, sa répartition dans cinq classes (inférieur à 0,2, 0,2-2, 1-20, 20-200 et supérieur à 200 μm), le temps de renouvellement du phosphate, la limpidité de l'eau (profondeur Secchi) et la biomasse du phytoplancton (chlorophylle a) ont été mesurés pendant deux étés dans huit grandes enceintes auxquelles on a ajouté des poissons planctonophages (perchaude 1+) et des éléments nutritifs (N et P) selon un plan d'expérience factoriel 2x2. On a également mesuré ces paramètres dans deux lacs de kettle mésoeutrophes. Dans l'un d'eux, les poissons planctonophages abondaient tandis que dans l'autre, ils étaient peu nombreux. L'un de ces deux lacs contenait les enceintes. Des données comparables ont également été recueillies dans trois lacs mésooligotrophes situés dans le centre de l'Ontario. Tant dans les enceintes que dans les lacs, une prédation intense de la part des poissons planctonophages a entraîné une augmentation du PT, une diminution de l'abondance des organismes zooplanctoniques de grande taille et du PP du mésoplancton (supérieur à 200 μm), une augmentation du PP du picoplancton et du nanoplancton (1-20 μm), une baisse des concentrations de phosphate (temps de renouvellement plus rapide), un accroissement de la teneur en chlorophylle a et une diminution de la limpidité de l'eau. L'addition d'azote et de phosphore dans les enceintes s'est traduite par une variabilité accrue quant aux relations entre les paramètres. Les traitements expérimentaux réalisés au cours de deux ans ont produit, sur le plan qualitatif, des effets similaires, mais l'importance de ceux-ci différerait en fonction des paramètres. D'après les résultats obtenus, les processus influant sur la répartition par taille et la biomasse du plancton dans les grandes enceintes utilisées à des fins d'expérimentation seraient fondamentalement similaires à ceux observés dans les lacs, et les enceintes constitueraient un outil fort utile pour l'étude des interactions complexes dans les écosystèmes aquatiques.

Abstract. Experimental manipulations of planktivorous fish in large enclosures produced plankton communities comparable to those in lakes with contrasting abundances of planktivorous fish. Total epilimnetic phosphorus (TP), its distribution among five size-classes of dissolved ($<0.2 \mu\text{m}$) and particulate phosphorus (PP $0.2 - 1$, $1 - 20$, $20 - 200$, and $>200 \mu\text{m}$), phosphate turnover time, water clarity (Secchi depth), and phytoplankton biomass (chlorophyll a) were measured for two summers in eight large enclosures where planktivorous fish (1+ yellow perch) and nutrients (N and P) were added in a 2×2 factorial design. These parameters were also measured in two meso-eutrophic kettle lakes, Lake St. George and Haynes Lake, containing low and high abundances of planktivorous fish, one of which was the lake (Lake St. George) containing the enclosures. Comparable data were also collected from three oligo-mesotrophic lakes in central Ontario. In both the enclosures and the lakes, intense planktivorous fish predation was associated with increased TP, decreased abundance of larger zooplankton and mesoplanktonic PP ($> 200 \mu\text{m}$), increased pico- and nanoplanktonic PP ($1 - 20 \mu\text{m}$), increased phosphate limitation (faster turnover time), increased chlorophyll a , and reduced water clarity. Slope parameter, an index of plankton size spectrum, was correlated with phosphate turnover time and Secchi depth among enclosures, and the data from all five lakes conformed to these empirical relationships. Fertilization of enclosures produced increased variability in the relationship among the variables. Our two years of experiments produced qualitatively similar treatment effects, but the magnitude of the effects was not similar for all parameters. We suggest that the responses of plankton communities and associated parameters to planktivore predation that we observed in large experimental enclosures are basically similar to those in the lakes we studied, and that enclosures are an important tool in understanding complex interactions in aquatic systems.

Introduction

Shifting the size of herbivorous zooplankton, either by adding or removing planktivorous fish or by physical addition or removal of larger zooplankton with screens in enclosures or lakes, have been found to change the biomass and community structure of phytoplankton, and water clarity. Various kinds and sizes of enclosures have been used, including small ones with closed bottoms (1 - 3 m diameter and 1 - 10 m deep; e.g., McCauley and Briand, 1979; Lynch and Shapiro, 1981; Riemann, 1985; Vézina, 1986; Bloesch et al., 1988; Prepas and Trimbee, 1988) and open bottoms (Tatrai and Istvánovics, 1986), and large ones with bottoms open at the sediment (8 m diameter and 15 m deep; McQueen et al., 1986; Post and McQueen, 1987; Mazumder et al., 1988; McQueen and Post, 1988). Others have used tanks with solid walls (Smith and Horne, 1988; Threlkeld and Søballe, 1988). Shifts in zooplankton size-structure have also been observed following whole lake manipulations of planktivorous fish (Shapiro, 1980; Lynch and Shapiro, 1981; Shapiro and Wright, 1984; Carpenter and Kitchell, 1988).

Controversy still exists regarding the value of results obtained from enclosure experiments (Bloesch et al., 1988; Carpenter and Kitchell, 1988). Recently, Bloesch et al. (1988) compared results from enclosures with data from the parent lake, and concluded that in "Control" enclosures eddy diffusion was smaller, nutrient depletion was greater, and phyto- and zooplankton standing crops were lower than those in the surrounding lake. Because there were no planktivorous fish in their enclosures, we question the expectation that the zooplankton and phytoplankton in the enclosures should resemble those found in the lake which did contain planktivores. Although enclosures without fish and with no other treatment, may be designated as "Controls" in the context of an experiment, it does not necessarily follow that these enclosures should resemble the surrounding lake. Lynch and Shapiro (1981) reported similar zooplankton and phytoplankton communities in

Control enclosures and the surrounding pond, but the surrounding pond did not have planktivorous fish. Further, Bloesch et al's manipulated (filtered) enclosures was also not comparable to the lake, because the plankton removed by a 95 μm filter were almost certainly different from those removed via selective predation by planktivorous fish. Lynch (1979) and Lynch and Shapiro (1981) demonstrated that physical removal of zooplankton reduced the abundance of all zooplankton species, whereas removal of zooplankton via predation reduced some zooplankton species, while other less vulnerable species increased in abundance.

Manipulation experiments in either enclosures or whole lakes have inherent advantages and disadvantages. Experiments can be adequately replicated in enclosures, but not in lakes. On the other hand, even the largest enclosures may not mimic lakes in several ways. For example, physical forces such as mixing process may be limited in enclosures. In addition, predation impacts from one type of planktivorous fish, as is the case for most manipulation studies in enclosures and whole lakes, may be different from the predation impacts of natural fish communities. Despite all the problems associated with enclosures, manipulation studies in enclosures provide information on the major processes regulating plankton communities. It is worthy to determine whether the responses of plankton communities to contrasting predation in enclosures are similar to those in natural lakes. Although enclosed systems have been widely used to investigate food web interactions, few studies compared enclosure results with the parent lake (Lynch, 1979; Lynch and Shapiro, 1981; Brabrand et al., 1987; Bloesch et al., 1988), and no studies have compared enclosures data with other lakes.

The purpose of this paper is to determine the impacts of contrasting planktivore predation on plankton community structure and associated parameters in large enclosures and lakes. Specifically, we examine whether the size-distribution and biomass of plankton

and associated parameters follow similar patterns in the enclosures with and without planktivorous fish, and in the lakes with high and low abundances of planktivorous fish. For the spring and summer of 1986, we demonstrated that marked changes in the size-distribution of planktonic PP can be caused by adding nutrients and/or planktivorous fish to large lake enclosures (Mazumder et al., 1988). From the size-distribution of PP, we developed a summary index (the slope of the relationship between the proportion of PP retained and the logarithm of filter-size) that was sensitive to our treatments and related to nutrient limitation (PO_4^{3-} turnover times) and water clarity. During the spring and summer of 1987, we repeated the enclosure experiment and collected comparable data from the parent lake, which had abundant planktivorous fish, and a nearby lake with few planktivores. Here we present data on zooplankton size-distribution, total phosphorus (TP), size-distribution of particulate phosphorus (PP), phosphate turnover time, water clarity, and chlorophyll *a* in the unfertilized enclosures with and without planktivorous fish. We also compare these parameters between two lakes with high and low abundances of planktivorous fish. Enclosure data were also used with data from three other Ontario lakes to see if lakes and enclosures conform to similar empirical relationships among variables such as water clarity, phosphate turnover time, index of plankton size-distribution. We have also compared enclosure results for both years to test the repeatability of enclosure experiments.

Materials and methods

Enclosure Experiments. Enclosure experiments were conducted in Lake St. George (43°57'30" N, 79°25'30" W), near Toronto, Ontario. Details of the enclosures and experimental design are described elsewhere (Mazumder et al., 1988). Briefly, eight large enclosures (8 m diameter, 15 m deep, and open at the sediment) were used. Nutrients (N

and P) and/or planktivorous fish (1+ yellow perch) were added (3 May) in a 2x2 factorial design with two replicate enclosures in each treatment. Treatments were Control (no additions), +F (with fish additions), +N (weekly nutrient additions), and +NF (both nutrient and fish additions). In each group of enclosures, fertilized and unfertilized, the enclosures with fish in 1986 were used as enclosures without fish in 1987 to eliminate any long-term effects of fish, although all fish were recovered after the experiment was terminated in September, 1986.

Fish stocks were 84 ($16,710 \text{ ha}^{-1}$) and 45 (8952 ha^{-1}) yellow perch per enclosure (50.27 m^2) in 1986 and 1987, respectively. Fish abundance in the parent lake (Lake St. George) for the year prior to the year of experiment was used for enclosures experiments. As we started our experiments in early spring, it was not possible to use current year's fish stock. In 1986, we used the fish stock of 1985 ($15,000$ to $20,000 \text{ ha}^{-1}$), and similarly in 1987, we used the fish stock of 1986 ($8,000$ to $10,000 \text{ ha}^{-1}$) (McQueen et al., 1989). Because of the continuous declines in the abundances of planktivorous fish during 1985 to 1987, our stocks in the enclosures were higher than the parent lake. However, our fish stocks were not unrealistic for meso-eutrophic lakes because Lake St. George had even higher abundances prior to 1985.

Description of lakes: Lake St. George and Haynes Lake are small meso-eutrophic kettle lakes, situated within 800 m of each other. Lake St. George has two basins, the west basin (4.1 hectares) where we worked is 15 m deep. The littoral zone has submerged macrophytes which extend about 1 to 20 m from the shoreline. In 1987, the planktivore population was 5510 planktivorous fish (yellow perch dominated) per hectare. Haynes lake (2.6 hectares), has a maximum depth of 16 m, is steep-sided and has very few submerged macrophytes in the littoral. This lake had 98 planktivorous fish (golden shiner dominated) per hectare. Jacks Lake (Sharpes Bay) is described in Hamilton and Taylor (1987), and

Plastic Lake ($3541 \text{ planktivores.ha}^{-1}$) is described in Yan and Mackie (1987). Johnson Lake is a large (150 ha) oligotrophic lake with low planktivorous fish abundance (61 ha^{-1}). Data on abundance of planktivorous fish are presented elsewhere (McQueen et al., submitted). All five lakes exhibit strong thermal stratification in late spring and summer.

Parameters measured: Details of collection and measurement procedures are described in Mazumder et al. (1988). All samples were collected from the epilimnion (4 m) of enclosures and lakes with a 0 - 4 m integrated tube sampler (6.5 cm diameter) on four dates during May through August of 1986 and 1987. Biomass and size-distribution of plankton were expressed as particulate phosphorus (PP) in six size-classes. On each date, two measurements were made from each enclosure (4 measurements per treatment). For the lakes, three measurements were made once every month.

Collected samples were filtered through Nuclepore™ filters (0.2, 1, and 3 μm pore sizes) and Nitex™ screens (20, 200, and 400 μm mesh sizes). Filtrate through 0.2 μm (for dissolved phosphorus), filters and screens containing plankton were analyzed for phosphorus after oxidation with potassium persulfate under pressure (Menzel and Corwin, 1965) with the ascorbic acid modification of the molybdenum blue method (Strickland and Parsons, 1972). Concentrations of phosphorus, dissolved ($< 0.2 \mu\text{m}$) and particulate phosphorus (PP) (0.2-1, 1-3, 3-20, 20-200, 200-400, and $>400 \mu\text{m}$) were measured. Total phosphorus was estimated by adding all the fractions.

In order to simplify the description of plankton size-distribution and to facilitate intersystem comparison of the entire size-spectrum of plankton, we developed an index (expressed as Slope) of plankton size-distribution (Mazumder et al., 1988). Slope, the index of plankton size-spectrum, was calculated by plotting the cumulative proportions of PP retained on each filter (0.2-, 1-, 3-, 20-, 200-, and 400- μm) against the logarithm of filter-size. The slope of this linear relationship was used as the index. Another index, the

median size of PP or MSP which is the filter size that divides total plankton biomass (PP) into two equal halves, was also calculated from this relationship (calculating x or filter-size given $y = 0.5$ or 50th percentile). We developed this index (Slope) because the indices of plankton size-spectrum developed by others, calculated from cumulative concentrations rather than cumulative proportions of either phosphorus (Peters, 1983) or plankton biovolume (Sprules et al., 1983) or seston biomass (Lean and Fricker, 1985), are sensitive to trophic status, but not to trophic level interactions. To solve this problem, we normalized our index for total biomass by using the proportions of total biomass in different size-classes. The usefulness of our Slope parameter to planktivore predation and fertilization has been demonstrated elsewhere (Mazumder et al., 1988). We found that this index is robust in indicating the impacts of predation and nutrient addition on plankton size-distribution and associated parameters such as water clarity and nutrient limitation. We also found that Secchi-chlorophyll relationship was improved when the Slope parameter was added as a second independent variable to the relationship.

Phosphate turnover time, an indicator of phosphate limitation, was determined using $^{32}\text{PO}_4^{3-}$ (Mazumder et al., 1988). Duplicate phosphate uptake experiments were conducted on 0-4 m integrated samples collected from each replicate enclosure. Three experiments were conducted on 0-4 m samples from the lakes. Carrier-free $^{32}\text{PO}_4^{3-}$ ($1.8 - 3.0 \text{ MBq ml}^{-1}$) was added to 100 ml of each sample in sterile 150 ml polycarbonate beakers. Aliquots (1 ml) were filtered through $0.2 \mu\text{m}$ Nuclepore filters (25 mm diameter) after 0.5, 1, 1.5, 2, 4, 6, and 10 min of incubation. After 15 min of incubation, 5 ml subsamples were filtered through 0.2 , 1 , 3 , and $12 \mu\text{m}$ Nuclepore filters to determine the size-distribution of assimilated phosphate isotope. Radioactivity on each filter and filtrate were determined by liquid scintillation counting. Uptake rate constants (k), the regression coefficients, were estimated by least-square regression of $\ln (\% ^{32}\text{P} \text{ remaining in solution})$ vs. time (min). The reciprocal of the absolute value of k is the turnover time (Lean 1973).

Concentrations of chlorophyll *a* (chl *a*) (2 measurement per treatment and 1 per lake) were measured from 0 - 4 m samples following Burnison (1980). Water clarity, expressed as Secchi depth, was measured using a 20 cm diameter Secchi disk. Zooplankton samples were collected at each meter depth from 0 to 12 m with a 35 liter Schindler trap. The averages of samples from 0 to 4 m were used here. This was done to keep consistency among all parameters measured from either enclosures or from lakes.

Statistical analyses: Statistical analyses were done using Systat (Wilkinson, 1986). To test the effects predation in the enclosures, one way analysis of variance (ANOVA) was performed on all the parameters. Repeated measures ANOVA were performed when data for all dates in each year were analyzed together, and the degrees of freedom were corrected accordingly (Zar, 1984). We used paired t-test to test that the parameters measured in Lake St. George was statistically different from those in Haynes Lake. Lake St. George and Haynes Lake were compared for TP, PP in different sizes, Slope, and turnover times on each date and for all dates together (May through August). Statistical comparisons (paired t-test) of Secchi and chl *a* between enclosures with and without fish, and between lakes with high and low abundances of planktivorous were made for all four dates together because single estimates were obtained for these parameters on each date.

Results

Abundances and size-distributions of zooplankton Crustacean zooplankton were larger in the enclosures without fish and also in the lake with low planktivores (Haynes Lake); they were common in the size-classes larger than 1 mm (Figure 1), and the seasonal mean lengths of *Daphnia* were 1.11 mm and 1.27 mm, respectively. In the +F enclosures, most of the zooplankton were smaller than 1 mm, and the mean length of *Daphnia* was 0.67 mm. In this enclosures (+F), all the zooplankton which were larger than 1 mm were

calanoids. Similarly, zooplankton in the lake with high planktivore abundance (Lake St. George) were small, and seasonal mean length of *Daphnia* was 0.69 mm. Lake St. George had much higher abundances of small zooplankton (rotifers, *Bosmina*, and *Ceriodaphnia*) compared to Haynes Lake. In the +F enclosures, these small zooplankton were more abundant than those in the control enclosures.

Total epilimnetic phosphorus and its size-distribution: Spring TP were similar in the enclosures with and without fish, and in the two lakes with high (Lake St. George) and low (Haynes Lake) abundances of fish. As the summer progressed, marked differences in TP were observed between treatments and between the two lakes. Total epilimnetic phosphorus (TP) was higher in the +F enclosures than in the Control enclosures on all dates except in spring (12 May) ($0.001 < P < 0.059$) (Table I). The high planktivore lake (Lake St. George) also had higher TP than in the low planktivore lake (Haynes Lake) on all dates ($.032 < P < 0.047$) except on 12 May. Seasonal mean TP was lower in the Control enclosures than in the +F enclosures (Table I). It was also lower in Haynes Lake. Declines in TP from spring to summer (May to August) were lower in the enclosures with fish ($P < 0.005$), and in the lake with high planktivore abundance ($P < 0.043$).

The contribution of different size-classes of phosphorus to TP was different in enclosures with and without fish, and in the lakes with low and high abundances of planktivorous fish (Figure 2). Total dissolved phosphorus concentrations ($< 0.2 \mu\text{m}$) were higher in the enclosures without fish than in +F enclosures on all dates ($0.019 < P < 0.048$) except on 23 June when they were similar in the two treatments ($P > 0.05$). Dissolved phosphorus was much higher in Haynes Lake than those in Lake St. George on all dates ($0.001 < P < 0.011$). In the enclosures, the contribution of pico- and nanoplanktonic PP (1 - 20 μm) to TP was 142% greater (on a seasonal basis) with fish than that without. In Lake St. George, it was 176% greater than that in Haynes Lake. The contribution of

microplanktonic PP (20 - 200 μm) was 21% higher in the enclosures with fish. In Lake St. George, it was 56% higher (seasonal means) than that in Haynes Lake. Mesoplanktonic phosphorus (> 200 μm) was 63% and 29% higher in the Control enclosures and in Haynes Lake, respectively.

Slope and MSP: Steeper slopes (more negative), observed in the enclosures with fish and the lake with high abundances of fish, indicate that plankton communities were dominated by pico- and nanoplankton, whereas shallower slopes, observed in the enclosures without fish and the lake with low abundances of fish, indicate that the plankton communities were dominated by micro- and mesoplankton. The slope parameter was steeper in +F enclosures than those in the Control enclosures on all dates ($0.007 < P < 0.012$) except 12 May (Table II). Lake St. George (high planktivore lake) had significantly steeper slopes than Haynes Lake (low planktivore lake) except on 23 June ($0.017 < P < 0.037$; Table II). Median size of PP (MSP), which divides the total epilimnetic PP into two equal halves, was smaller (more smaller plankton) in the enclosures with fish, and in Lake St. George. The slope parameter appears to be more stable than the MSP parameter.

Phosphate turnover times: Phosphate turnover time (Table III) was significantly faster (i.e., more severe phosphate limitation) in +F enclosures than in the Control enclosures on all dates ($0.011 < P < 0.029$) except on 12 May. In Lake St. George it was much faster than those in Haynes Lake on all dates ($0.001 < P < 0.021$). When data on phosphate turnover time and the slope parameter for two years from enclosures with four different treatments, for Lake St. George and Haynes Lake, and for 3 other Ontario lakes were combined, a significant negative relationship was obtained (Figure 3), indicating that faster turnover times are associated with steeper slopes in enclosures and in lakes with high abundance of planktivorous fish. The data from fertilized enclosures without fish were more variable than for other treatments and lakes.

*Water clarity (Secchi depth) and phytoplankton biomass (Chlorophyll *a*):* In the enclosures without fish, water clarity, measured as Secchi depth, was significantly greater on all dates except on May 12 ($P < 0.005$). In Lake St. George, water clarity was two to three times lower than that in Haynes Lake on all four dates (Table IV). Seasonal mean for Secchi depth was also lower in Lake St. George ($P < 0.005$). When data on Secchi depth and slope parameter for two years from four treatments, and for Lake St. George and Haynes Lake were combined, a significant negative relationship ($P < 0.001$) was obtained (Figure 4); steeper slopes, which indicate pico- and nanoplankton dominated communities, were associated with lower water clarity.

Phytoplankton biomass, expressed as chlorophyll *a* (chl *a*) concentration, was higher in the enclosures with fish on all dates ($0.003 < P < 0.007$), except 12 August (Table V). Lake St. George had several times higher concentrations of chl *a* than Haynes Lake on all dates. On a seasonal basis, chl *a* concentrations were 178% higher in the enclosures with fish than those without. It was over 500% higher in Lake St. George than in Haynes Lake ($P < 0.005$).

Comparison of two years data from enclosures: Treatment effects were similar between years (Table VI). Of 44 possible pair-wise comparisons, only 6 showed different qualitative effects of the treatments for the two years. Most of the comparisons which were different between the two years were only marginal changes from the Control enclosures. None of the qualitative differences between years involved the Control versus fish addition (+F) treatments, but the magnitude of the differences, or quantitative effects of the treatments were often different for the two years of experiments.

Discussion

Responses of plankton community and associated parameters to contrasting planktivore predation followed a similar pattern in enclosures and lakes. In the enclosures with fish and in Lake St. George, high planktivore predation reduced the abundance of large zooplankton which were associated with high concentrations of pico- and nanoplankton biomass. These changes were associated with high chl *a*, reduced water clarity, and more severe nutrient limitation. Therefore, the impacts of planktivore predation on plankton community structure and associated parameters were similar for both enclosures and in the two lakes during our study period of spring through summer. The only similar study that compared enclosure data with the surrounding lake (Bloesch et al., 1988) found that parameters measured from enclosures (Control and filtered) were different from those measured from the lake, and this led the authors to question the value of enclosure experiments.

Our slope parameter, the index of plankton of plankton size-distribution which we developed from enclosures with contrasting abundances of planktivores (Mazumder et al. 1988), clearly indicates the impacts of contrasting planktivory among lakes. The slope parameter, which is sensitive to planktivore predation and fertilization, was significantly correlated with phosphate turnover time and Secchi depth (Figures 3 & 4). A steeper or larger slope, observed in the enclosures with fish and in the lakes with high abundances of fish, indicates that the plankton community is dominated by pico- and nanoplankton, which are associated with high nutrient limitation and low water clarity. Our enclosure data conform to the same empirical relationships as five whole lakes, suggesting that the responses of plankton community and associated parameters to planktivore predation were similar among large enclosures and lakes. These relationships also suggest that slope may be a robust parameter indicating planktivore predation or trophic level interactions in lakes.

However, more data are needed from a large number of lakes with wide range of trophic status and planktivore abundance, to test this idea.

Like Bloesch et al. (1988) we found our Control enclosures to be dissimilar to the parent lake. However, our lake versus enclosure comparison suggest that differences between "Control" enclosures and the parent lake are not due to the enclosures *per se*. Rather the expectation that Control treatments should resemble the lake is questionable. Although enclosed natural populations are referred to as "Control" in the context of an experiment, they cannot be compared to the lake, because they exclude fish. In our case, the +F enclosures had similar size-distribution of plankton, and associated water clarity and nutrient limitation to the parent lake (Lake St. George). Although our fish stocks in the enclosures were higher than the surrounding lake, large cladocerans (especially large *Daphnia*), high abundances of which are often responsible for decline in algal biomass, were totally eliminated in both enclosures with fish and in the surrounding lake. The responses of pico- and nanoplankton to the total elimination of large grazers were similar in the enclosures with fish and in the surrounding lake. Our Control enclosures differ from the parent lake, although we filled the enclosures with water from the lake, but resemble a nearby lake (Haynes Lake) with few planktivorous fish.

It is often impossible to compare enclosures with or without fish to the surrounding lake, because the fish population of the lake is not known (e.g., Riemann, 1985; Geertz-Hensen et al., 1987). However, in these two studies, the biomass of zooplankton, chlorophyll concentration, and bacterial biomass in the lake was more similar to the enclosures with fish than to the Control enclosures.

Imitating the effect of size-selective predation by planktivorous fish by filtering out zooplankton with a screen (e.g. McCauley and Briand, 1979; Uehlinger et al., 1984; Bergquist et al., 1985; McCauley and Kalff, 1987; Uehlinger and Bloesch, 1987a, 1987b;

Bloesch et al., 1988) presents problems because a screen removes all the zooplankton larger than the mesh size used, and this may be substantially different from removal of zooplankton by fish. Removing zooplankton by screens eliminates the competition between small and large zooplankton, we observed that in the enclosures and in the two lakes small zooplankton were more abundant when planktivores selectively removed the large zooplankton. Lynch and Shapiro (1981) demonstrated that planktivorous fish predation produced a significantly different size-distribution of herbivorous zooplankton compared to that produced by physical removal of zooplankton by screening. In addition, it is not possible to conduct seasonal (spring through summer) manipulation experiments by removing zooplankton with screens because smaller juvenile stages may grow into large adults and obscure the manipulation effects. On the other hand, short-term (few weeks) experiments may not provide enough time to show manipulation effects at lower trophic levels.

Extrapolation of short-term enclosure experiments to whole-lake dynamics can lead to major errors (Carpenter and Kitchell, 1988). Total phosphorus, slope parameter, and phosphate turnover time measured during our experiment were similar in the Control and +F enclosures even 2 weeks (12 May) after manipulation was started. As our manipulation progressed in time, we found that fish, by changing the size-distribution of plankton, can change nutrient limitation, while McCauley and Briand (1979), Hamilton and Taylor (1987), and McCauley and Kalff (1987) found little or no effect of mesozooplankton manipulation on phosphate turnover time during short-term manipulation experiments. Results from other seasonal studies (spring through summer) also indicate that alteration of food web structure by adding or removing fish may change nutrient limitation of freshwater plankton (Tatrai and Istvánovics, 1986; Elser et al., 1988).

In many studies, comparison of enclosures with the surrounding lake is difficult because nutrients are added to the enclosures as part of the background maintenance of the enclosures; it is a common practice to fertilize the enclosures, with the idea being that enclosures need additional nutrient supply in order to prevent nutrient depletion (Bloesch et al., 1988). Our data on zooplankton biomass and turnover time suggest that the low phytoplankton biomass generated in enclosures without fish is largely due to zooplankton grazing, and may not be only due to nutrient limitation. Fishless (Control) enclosures with abundant large zooplankton had lower TP and high spring to summer TP declines, and nutrient limitation was relaxed. A similar pattern was observed in Haynes Lake with few planktivorous fish. We will provide results on zooplankton grazing in our enclosures in a subsequent paper.

Elsewhere, we have demonstrated that planktivore predation can reduce sedimentation rates and spring to summer decline in TP by allowing the pico- and nanoplankton to dominate the plankton community, and by increasing the retention time of particles in epilimnion (Mazumder et al. 1989). The control enclosures had higher sedimentation rates and spring to summer decline of TP was higher. Although Lake St. George and Haynes lake had similar spring TP, the seasonal mean TP was much lower and spring to summer decline was greater in Haynes Lake where planktivore predation was low. This observation is consistent with our enclosure results. The higher TP decline in Haynes Lake may have been due to higher sedimentation ($\% \text{ TP} \cdot \text{d}^{-1}$). We do not have any data on the external P loading to these two lakes. However, our estimates for spring TP would suggest that both lakes received similar P loading during spring runoff and turnover. We also could not test whether a higher spring to summer mean TP and lower TP decline in Lake ST. George was due to higher loading of P, internal or external, during the stratified period.

Our two years of experiments following the same design except for the fish density (lower density in 1987) suggest that the results are robust. Other parameters we measured in the enclosures but not in the lakes, such as sedimentation of P (Mazumder et al. 1989) and zooplankton community grazing (unpublished data), showed similar manipulation effects in both years. However, the magnitude of differences between treatments and Control enclosures was not similar for both years for all parameters. Year to year variation is common in lakes (reviewed in Wetzel, 1975; Carpenter et al., 1987). However, the differences observed here could also be due to the different fish densities we used.

We conclude that enclosures can be used as an important tool to investigate trophic interactions in aquatic systems. Although enclosures obviously differ from lakes in many respects, the responses of plankton communities and associated parameters (e.g., water clarity, algal biomass, phosphate limitation, total phosphorus, its size-distribution or the slope and spring to summer declines in TP) we observed within our enclosures by excluding or adding fish were very similar to the two lakes with low and high abundances of planktivorous fish. In addition, the conformation of lakes and large enclosures to the same empirical relationships among variables, the slope parameter, Secchi depth and turnover time, also suggest that the responses of plankton community and associated parameters are similar in large enclosures and lakes. We therefore conclude that the impacts of planktivore predation on plankton communities in large enclosures follow basically similar patterns to those in natural lakes, at least to the lakes we studied.

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Table I. Mean epilimnetic TP estimated by adding all size classes of dissolved and particulate P in different treatments and lakes for 1987. Error estimates for enclosure data are 95% CI from 4 estimates (2 from each replicate enclosure) during May through August. Error estimates for lakes are 95% CI from three measurements each lake. HL = Haynes Lake; LSG = Lake St. George.

	Control	+F	HL	LSG
12 May	29.3 \pm 8.5	31.3 \pm 2.9	24.5 \pm 1.2	26.9 \pm 3.9
23 Jun	14.5 \pm 1.5	23.1 \pm 2.7 [†]	20.9 \pm 2.4	22.5 \pm 3.0*
13 Jul	14.0 \pm 2.6	23.0 \pm 1.9 [†]	17.9 \pm 2.4	32.8 \pm 2.1*
12 Aug	12.5 \pm 0.9	16.9 \pm 1.6 [†]	12.4 \pm 0.5	24.7 \pm 3.4*
Mean	17.6	23.6 [†]	18.9	26.7*

[†] indicates significantly different (ANOVA, $P < 0.05$) TP in enclosures with and without fish. * indicates that TP was significantly different (Paired t-test, $P < 0.05$) in Lake St. George than that in Haynes Lake.

Table II. Slope and Median Size of PP (in parentheses) in enclosures and lakes during May through August in 1987. $n = 4$ for enclosures (2 per replicate enclosure), and 3 for lakes.

HL and LSG are same as in Table I.

	Control	+F	HL	LSG
12 May	0.28 (10.3)	0.30 (6.0)	0.26 (7.3)	0.30* (5.7)
23 Jun	0.21 (8.8)	0.29 [†] (4.1)	0.26 (6.2)	0.27 (4.6)
13 Jul	0.21 (11.5)	0.30 [†] (6.7)	0.22 (31.8)	0.27* (4.5)
12 Aug	0.20 (12.5)	0.30 [†] (5.2)	0.22 (19.8)	0.27* (4.1)
Mean	0.23 (10.8)	0.30 [†] (5.5)	0.24 (16.3)	0.28* (4.7)

[†] and * are same as in Table I.

Table III. Phosphate turnover times (minutes) in enclosures and lakes from May through August in 1987. Error estimates are 95% CI. $n = 4$ for enclosures (2 per replicate enclosure), and 3 for lakes. HL and LSG are same as in Table I.

	Control	+F	HL	LSG
12 May	2.4 ± 0.5	3.3 ± 1.7	34.3 ± 4.5	$2.1 \pm 0.9^*$
23 Jun	19.8 ± 4.9	$7.0 \pm 1.2^\dagger$	8.5 ± 1.8	$4.0 \pm 0.0^*$
13 Jul	10.1 ± 1.9	$4.0 \pm 0.9^\dagger$	6.3 ± 0.9	$3.5 \pm 0.9^*$
12 Aug	13.5 ± 1.1	$6.5 \pm 1.1^\dagger$	9.1 ± 2.4	$2.9 \pm 0.7^*$
Mean	11.5	5.2^\dagger	14.6	3.1^*

† and * are same as in Table I.

Table IV. Water clarity expressed as Secchi depth (m) in the enclosures without and with fish and in the lakes with low (Haynes lake) and high (Lake St. George) abundances of planktivorous fish from May through August in 1987. HL and LSG are same as in Table I. $n = 2$ for enclosures (1 per replicate enclosure), and 1 for lakes. No statistical comparison was done for individual date for Secchi depth in lakes because estimates are based on a single measurement.

	Control	+F	HL	LSG
12 May	2.95	2.18	5.18	1.33
23 Jun	4.69	2.64 [†]	3.98	1.78
13 Jul	5.63	1.82 [†]	3.44	1.51
12 Aug	6.10	2.88 [†]	4.49	1.43
Means	4.84	2.38 [†]	4.27	1.51**

[†] is same as in Table I; ** paired t-test, $P < 0.005$.

Table V. Phytoplankton biomasses expressed as chlorophyll *a* concentration ($\mu\text{g. liter}^{-1}$) in the enclosures without and with fish and in the lakes with low (Haynes lake) and high (Lake St. George) abundances planktivorous fish from May through August in 1987. HL and LSG are same as in Table I. No statistical comparison was done for individual dates for chl *a* concentrations in lakes because estimates are based on a single measurement.

	Control	+F	HL	LSG
12 May	4.4	9.7 [†]	0.5	11.5
23 Jun	1.2	2.8 [†]	0.8	5.7
13 Jul	1.9	2.6 [†]	2.5	6.7
12 Aug	1.9	1.6	1.4	4.3
Means	2.4	4.2 [†]	1.3	7.1 ^{**}

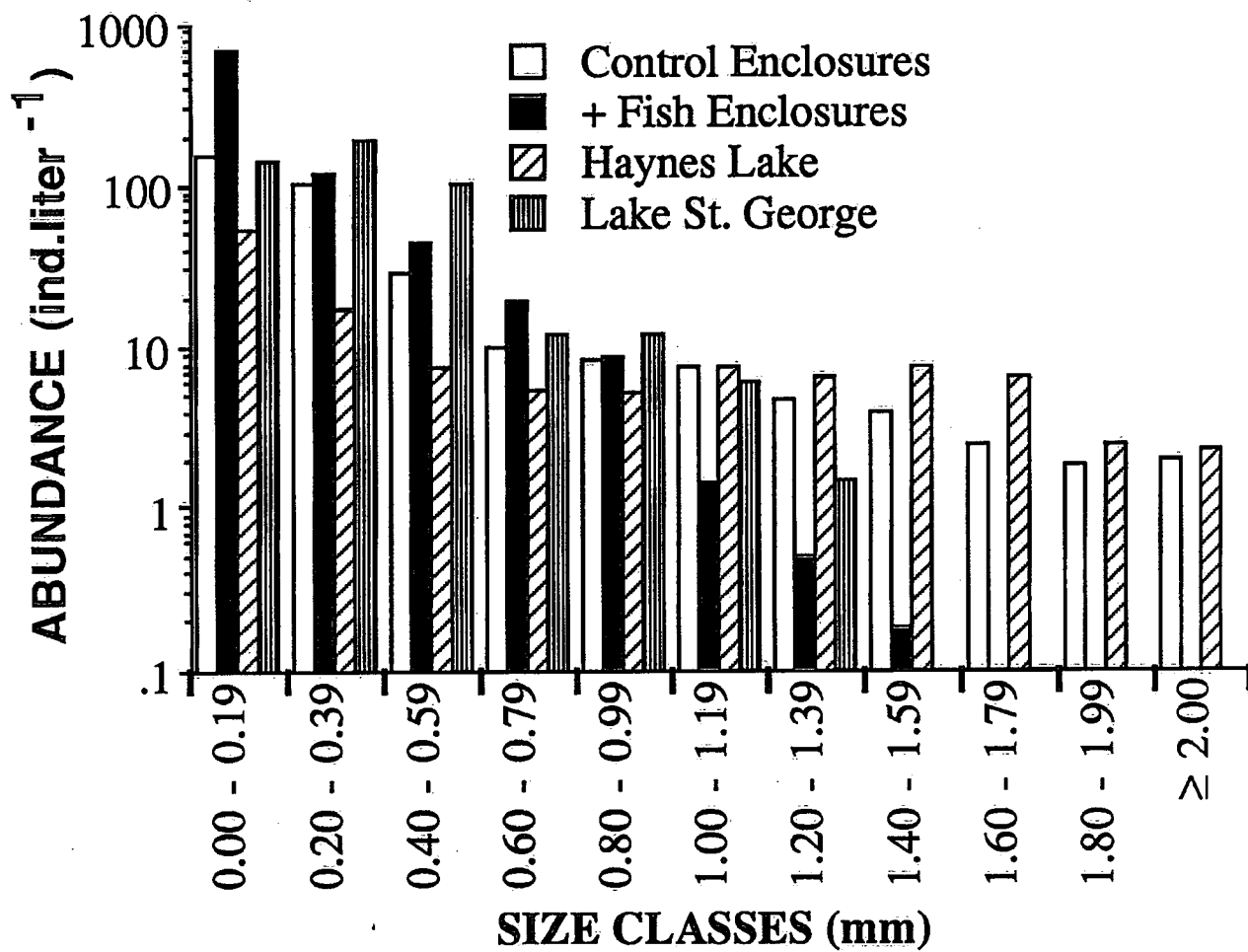
[†] is same as in Table I. ^{**} is same as in Table IV.

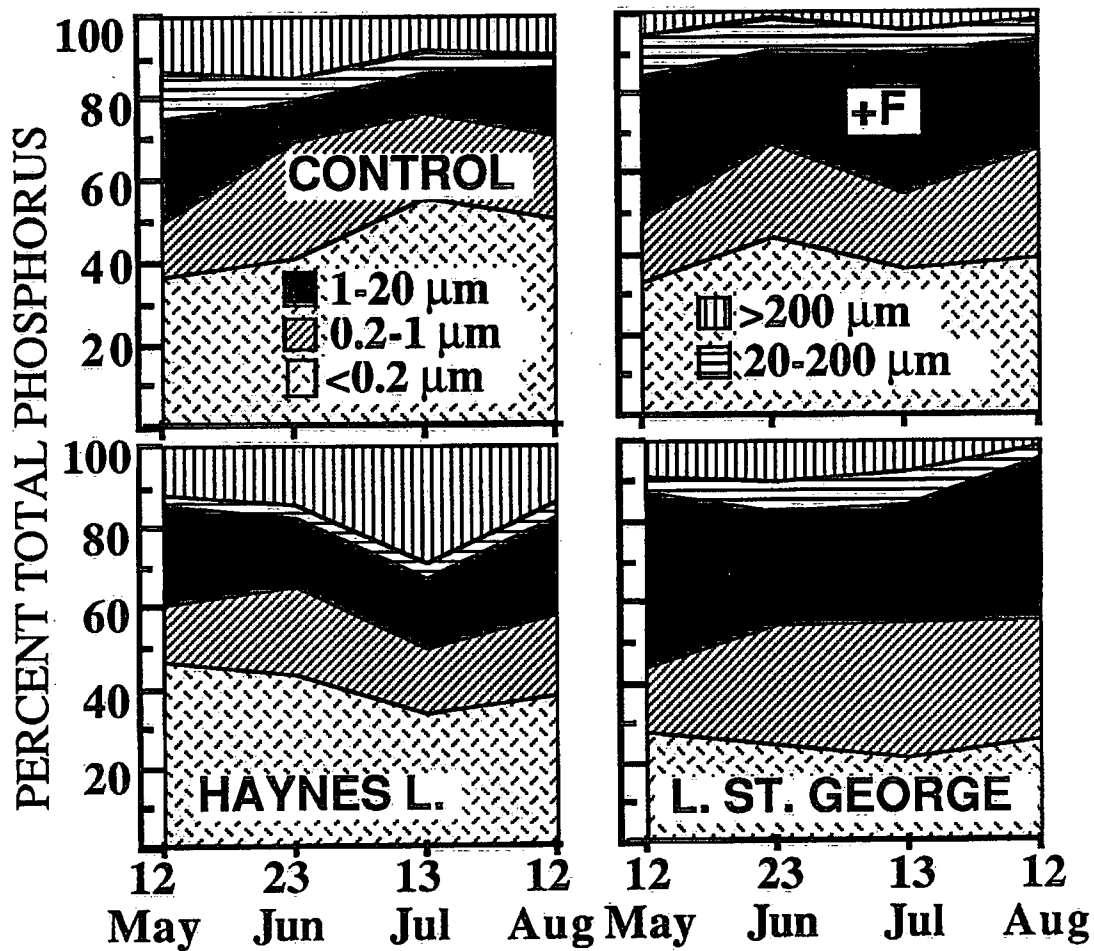
Table VI. Seasonal means of total phosphorus ($\mu\text{g P.l}^{-1}$) and its size-distribution (% of TP), slope, Median Size of PP, turnover time (TT), Secchi depth (m) and chl *a* ($\mu\text{g.l}^{-1}$) in the Control enclosures for 1986 and 1987, and comparison of different treatments. '+' and '-' indicate percent higher and lower, respectively. Top and bottom rows for each parameter are for 1986 and 1987, respectively.

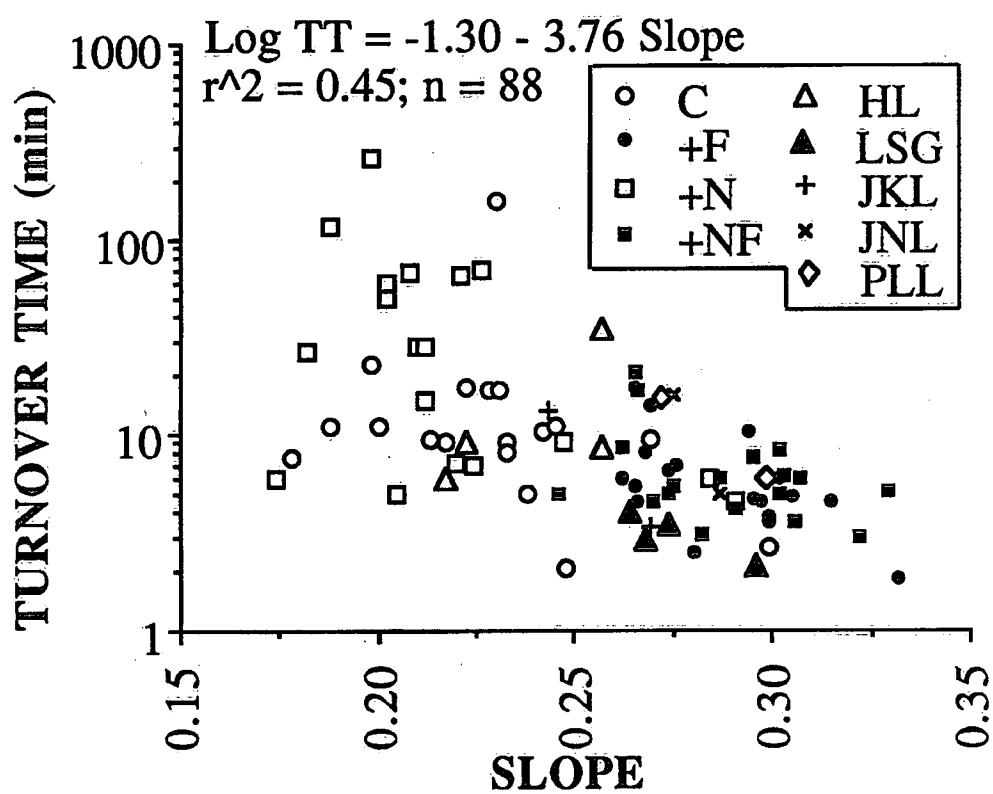
	Control (C)	C vs +F	C vs +N	C vs +NF	+N vs +NF
TP	16.74 17.35	+ 20.4% + 31.6%	+ 60.3% + 60.5%	+ 35.0% + 42.2%	- 35.0% - 11.4%
< 0.2 μm	6.9 (41.1%) 8.0 (46.1%)	+ 8.6% + 8.9%	+ 52.9% + 44.7%	+ 10.6% - 5.5%	- 17.7% - 34.7%
0.2 - 1 μm	2.3 (13.4%) 3.7 (21.1%)	+ 59.3% + 31.5%	+ 59.7% + 30.7%	+ 22.9% + 45.2%	- 23.0% + 11.1%
1 - 20 μm	1.2 (8.4%) 2.9 (16.6%)	+ 244.5% + 142.4%	+ 111.6% + 73.6%	+ 336.2% + 220.1%	+ 106.2% + 84.4%
20 - 200 μm	2.3 (13.8%) 1.1 (6.2%)	+ 21.1% + 36.8%	+ 70.7% + 35.2%	- 3.4% + 55.6%	- 43.4% + 15.1%
> 200 μm	3.9 (23.4%) 1.7 (10.0%)	- 51.1% - 63.2%	+ 42.5% +174.1%	-0.5% -37.6%	- 24.4% -76.8%
Slope	0.22 0.23	+ 27.3% + 30.4%	- 2.2% - 4.3%	+ 25.9% + 34.8%	+ 28.8% + 40.9%
MSP	32 11	- 71.9% - 36.0%	+ 50.0% + 96.5%	- 59.4% - 50.0%	- 72.9% - 74.6%
TT	25 11	- 68.0% - 54.8%	- 8.0% + 542%	- 64.0% - 46.0%	- 60.9% - 91.6%
Secchi	5.7 4.7	- 43.6% - 58.0%	- 27.8% + 5.3%	- 60.1% - 60.2%	- 44.4% - 62.2%
Chl <i>a</i>	3.1 2.4	+ 49.8% + 68.3%	+ 43.5% + 65.6%	+ 227.4% + 116.6%	+ 128.1% + 30.8%

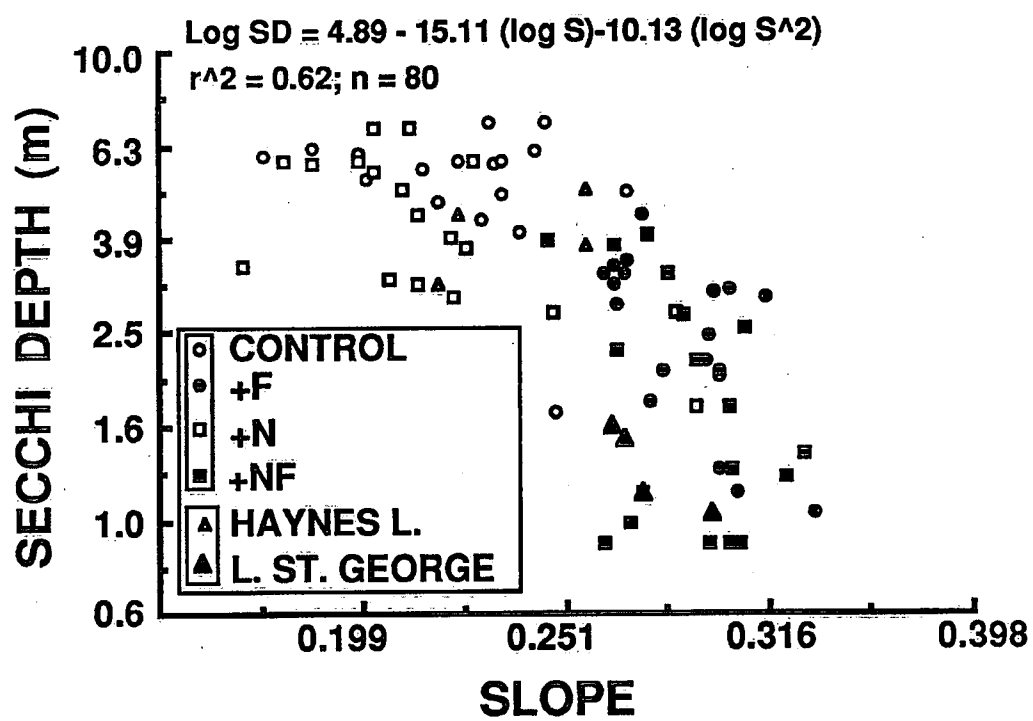
List of figures

- Fig. 1. Seasonal mean (spring through summer) abundances of total zooplankton (log scale) for 1987 (including cladocerans, copepods, nauplii and rotifers) in different size-classes for two treatments (with and without planktivorous fish), and in Lake St. George and Haynes Lake.
- Fig. 2. Size-distribution of total phosphorus (% of TP) for 1987 in two treatments (with and without planktivorous fish) and two lakes (high and low abundances of planktivorous fish). Each point is a mean of four determinations for enclosures and of three determinations for lakes.
- Fig. 3 Relationship between slope and phosphate turnover time (TT) for four treatments in enclosures (1986 and 1987) and five Ontario lakes (1987 only). LSG= Lake St. George, HL = Haynes Lake. JCL = Jacks Lake, JNL = Johnson Lake, and PLL = Plastic Lake. The Y-axis is in log scale. Data for 1986 are in Mazumder et al. (1988).
- Fig. 4. Relationship between slope (S) and Secchi depth (SD) for four treatments in enclosures (1986 and 1987) and two lakes (1987 only). Abbreviations associated with symbols are same as figure 3. Both axes are in log scale.











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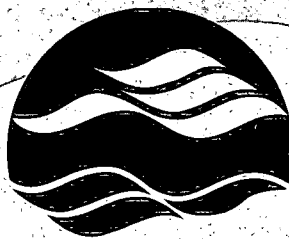
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