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Abstract

Over the past 15 years a great deal of literature has been generated in an attempt to understand the regulation of trophic level biomass and size structure in aquatic systems. It has been shown that both resources and predation can play important roles in regulating what we observe. However the extent to which biomass and size structure depend upon each process remains contentious. I tested the hypotheses that the among-lake variability in biomass and size structure of planktivorous fish, zooplankton, and phytoplankton communities depends on: 1. resource availability (bottom-up processes); 2. piscivorous sport fish stocking (top-down processes); and 3. the particular species of piscivorous sport fish stocked. We sampled 31 lakes in southeastern Ontario over the summers of 1993 and 1994 to obtain indices of abundance, biomass, and size structure of the planktivorous fish, zooplankton, and phytoplankton communities. Seven of the lakes were not stocked and the remaining 24 had stocking intensities ranging from 30 to 1500 individuals stocked per hectare over the 6 years prior to sampling. For both bottom-up and top-down analyses, trophic interactions were strongest at the base of the food web and weakened at higher levels, becoming non-significant thereafter. From these results I conclude that: 1. piscivorous sport fish stocking as a whole (at least at the magnitude examined here) had no effect on planktivorous fish, zooplankton, and phytoplankton biomass or size structure; 2. rainbow trout (*Oncorhynchus mykiss*) stocked lakes differ at the zooplankton and phytoplankton level from lakes stocked with other species of piscivore; 3. trophic interactions are most evident at the base of the food web (at the zooplankton and phytoplankton level); and 4. resource control (especially total phosphorus) of biomass and size structure in aquatic communities is much more important than consumer control, and it is limited to the phytoplankton and zooplankton. Our results suggest that stocking with piscivorous fish (as practised for sport fishing purposes) does not effectively manipulate plankton abundance.

Résumé

Au cours des 15 dernières années une ample de littérature a été générée dans le but d'essayer de comprendre la régulation de la biomasse et de la distribution en taille des niveaux trophiques des écosystèmes aquatiques. Les études antérieures ont démontré que les ressources et la prédation jouent tous les deux des rôles dans la régulation de ce qu'on observe. Toutefois l'importance de la biomasse et de la distribution des tailles sur chaque processus reste litigieuse. Nous avons examiné les hypothèses que la variabilité entre les lacs de la biomasse et de la distribution en taille des communautés de poissons planctivores, de zooplancton et de phytoplancton dépendent de: 1. la disponibilité des ressources (processus "bottom-up"); 2. l'introduction de poissons sportifs piscivores (processus "top-down"); et 3. les espèces de poisson utilisées pour l'alevinage. Au cours des étés de 1993 et 1994, nous avons échantillonnés 31 lacs du sud-est ontarien afin d'obtenir des indices d'abondance, de biomasse et de distribution en taille des communautés de poissons planctivores, de zooplancton, et de phytoplancton. Sept lacs n'étaient pas alevinés et les 24 autres avaient des intensités d'alevinage variant entre 30 et 1500 individus ajoutés par hectare au cours des 6 années précédant l'échantillonnage. Nous avons trouvé que pour les deux analyses, soit "bottom-up" et "top-down", les interactions trophiques étaient plus fortes à la base de la chaîne alimentaire et faiblissaient par la suite au point de devenir non significatif. De ces résultats on conclut que: 1. la manipulation de poissons sportifs piscivores (à l'échelle examinée) et sans égard pour les espèces utilisées est incapable d'affecter la biomasse ou la distribution des tailles des communautés de poissons planctivores, de zooplancton, ou de phytoplancton; 2. les lacs ensemencés avec la truite arc-en-ciel (*Oncorhynchus mykiss*) diffèrent des lacs ensemencés avec d'autres espèces en ce qui a trait au phytoplancton et au zooplancton; 3. les interactions trophiques sont plus évidentes à la base de la chaîne alimentaire (niveaux du zooplancton et du phytoplancton); et 4. comparé au contrôle effectué par des consommateurs, le contrôle des ressources (surtout de phosphore total) est beaucoup plus susceptible d'influencer la biomasse et la distribution en taille des communautés aquatiques. Les effets sont limités au phytoplancton et au zooplancton. Nos résultats suggèrent que l'alevinage des poissons piscivores n'est pas une méthode efficace pour manipuler l'abondance du plancton.

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Introduction

One of the fundamental problems in ecology is to determine what influences the abundance and size structure of organisms in natural communities (Fretwell 1987). In aquatic ecosystems, it is clear that the abundance of organisms is related to the availability of resources (i.e. nutrients or food) (Dillon and Rigler 1974, Elser et al. 1990). Statistical models have demonstrated that the variation among lakes in the abundance of bacteria (Currie 1990), phytoplankton (Dillon and Rigler 1974), zooplankton (McCauley and Kalff 1981, Hanson and Peters 1984), and fish (Hanson and Leggett 1982) are related to total phosphorus concentration (a measure of trophic status).

Trophic status is also an important mediator of size structure in phytoplankton (Sprules and Munawar 1986, Richman and Sager 1990) and zooplankton communities (Bays and Crisman 1983, Richman and Sager 1990). Along a gradient of increasing productivity, the phytoplankton shift towards a community dominated by large (> 35μm) netplankton, with smaller (< 35 μm) nanoplankton comprising a lesser proportion of the total algal biomass (Watson and Kalff 1981, Sager et al. 1987). Zooplankton community size structure in less fertile systems tends to be dominated by large-bodied crustacean zooplankton with few microzooplankton (rotifers and copepod nauplii), while richer systems tend to have smaller bodied crustaceans and a higher percentage of microzooplankton (McNaught 1975, Bays and Crisman 1983).

Despite the ubiquity of these "bottom-up" models and the substantial amounts of inter-lake trophic level variation they may explain, there remains a significant portion of residual variation that is unaccounted for (Carpenter et al. 1985). One model that has been proposed to account for the residual variation in abundance and community size structure is that of "cascading trophic interactions" (Carpenter et al. 1985, Carpenter and Kitchell 1993). This model proposes that the residual variation of the bottom-up models for both abundance and size structure of all trophic levels can be explained by differences in food web structure. The rationale is that piscivorous fish (secondary carnivores) eat planktivorous fish (primary carnivores), planktivorous fish eat zooplankton (herbivores), and zooplankton eat phytoplankton (primary producers). Lakes with more piscivores should have fewer planktivores, more zooplankton, and less phytoplankton than lakes with fewer or no piscivores. Thus, lakes which are piscivore-dominated should have less chlorophyll *a* per unit total phosphorus than predicted (i.e. negative residuals), and planktivore-dominated lakes should have more chlorophyll *a* per unit total phosphorus than predicted (i.e. positive residuals). It has also been suggested that manipulation of the abundance of the top piscivores could be a cost-effective method of reducing phytoplankton biomass, independently of nutrient levels (reviewed in Reynolds 1994)

The cascading trophic interactions hypothesis has been tested principally by manipulating a specific trophic level. For example, piscivorous fish (Benndorf et al. 1984), planktivorous fish (McQueen et al. 1986) or zooplankton (Theiss et al. 1990), densities are changed in small lakes or enclosures and shifts in trophic structure are compared to a reference or control system (Carpenter and Kitchell 1993, Proulx et al. 1996). Results from enclosure studies are at least partially consistent with the predictions of the trophic cascade hypothesis (as reviewed by DeMelo et al. 1992). Zooplankton densities can be reduced and phytoplankton densities increased in the presence of planktivorous fish (Hambright et al. 1986, Mazumder et al. 1988). However, the use of enclosures to study trophic interactions has recently been questioned (Carpenter and Kitchell 1992). Nutrient regeneration by planktivorous fish in enclosures may affect zooplankton and phytoplankton as much or even more than does predation (Threlkeld 1988, McQueen et al. 1992). Increases in phytoplankton biomass may be due entirely to greater nutrient cycling in enclosures containing fish (Vanni and Findlay 1990). Trophic cascades may not exist away from these heavily manipulated experimental systems (Crowder et al. 1988, Elser et al. 1995). Furthermore, criticism has been levelled at enclosure studies for having insufficient manipulation times (Power 1992, Carpenter and Kitchell 1992) thereby not allowing for several generations at the top trophic levels to occur. This is important as effects on the community as a whole may not be observed until a number of generations have occurred.

A second, more general way to test the cascading trophic interaction hypothesis, and to avoid some of the problems listed above, is to compare many lakes differing in food web structure. One can then relate the residuals from bottom-up models to differences in predator characteristics or trophic structure. This approach has been used to compare lakes with differing abundances of piscivorous and planktivorous fish (Mills et al. 1987, Quirós 1990), or zooplankton (Pace 1984), as well as lakes having food webs with different numbers of functional groups or trophic levels (Persson et al. 1992, Mazumder 1994). These studies have generally concluded that it is possible to relate some among-lake variation in trophic level biomass to differences in food web structure. However, lakes with contrasting predator assemblages often also differ markedly in physical and chemical characteristics. Thus the among-lake variability in plankton biomass associated with contrasting fish assemblages may result from parallel gradients of abiotic factors (Arnott and Vanni 1993).

One aspect of the multi-lake comparison type approach that has not been examined, however, is the combination of the empirical and manipulation studies outlined above. By studying a trophic level manipulation across a number of lakes, it is possible to integrate these two approaches while eliminating some of the confounding factors associated with them. This can be carried out by examining lakes along a gradient of trophic level manipulation.

Piscivorous sport fish stocking programs provide an among-lake trophic level manipulation that allows one to test the cascading trophic interactions hypothesis. Piscivorous sport fish stocking is a wide-spread practice in southern Ontario. The goals of the program are to provide a viable sport fishery for the public. However, the program also provides a test of the cascading trophic interaction hypothesis, since it is a sustained and long term manipulation of the fish community. The lakes in my study have been stocked annually for at least 6 of the last 10 years, thus eliminating the problem of insufficient manipulation time (Carpenter 1989). Secondly, the annual stocking of piscivorous sport fish allows for a constant (press versus pulse) manipulation of the food web which prevents shifts in food web structure from dissipating as the manipulated year class decreases over time. This is important if the goal of a study is to make a manipulation "stable" and long lasting (Shapiro 1990, Meijer et al. 1994). Moreover, such stocking is exactly the type of biomanipulation that has been proposed for phytoplankton management purposes (Benndorf 1987, 1990).

It has furthermore been shown that the species of predator in a system may have implications for trophic interactions. Different species of planktivorous fish (Drenner et al. 1986, Novales-Flamarique et al. 1993) and zooplankton (Brett et al. 1994) have different impacts on their prey. If this is also true for different species of piscivorous sport fish, it could have implications for the cascading trophic interactions hypothesis. In this study, we examine non-stocked (or unmanipulated) lakes as well as lakes stocked with four different species of piscivores: lake trout (*Salvelinus namaycush*), splake (F1 *S. namaycush* X *S. fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and yellow walleye (*Stizostedion vitreum*). Coldwater species such as lake trout are limited to the hypolimnion of lakes over the summer months, whereas warmwater species such as walleye may forage in the warmer epilimnion and littoral zone areas. Furthermore, the dietary habits of the species stocked vary markedly, with rainbow trout tending towards omnivory, and walleye being almost exclusively piscivorous. These different life history traits, habitat, and diet choices (Scott and Crossman 1973), have the potential to alter the magnitude and propagation of top-down trophic cascades.

The purpose of this study is to test three sets of hypotheses. First, we hypothesize that consumer biomass and size structure are dependent on resource availability. Therefore, I expect to observe an increase in consumer trophic level biomass with increasing trophic status (total phosphorus) and prey abundance (Fig. 1, top). I also predict that consumer size structure is dependent on trophic status and prey abundance (Fig. 1, bottom), based principally on the empirical patterns described above.

Second, we hypothesize that, along a gradient of piscivore stocking (i.e. piscivore manipulation), there exist corresponding gradients in planktivore, zooplankton, and phytoplankton abundance and community size structure, independent of total phosphorus concentration. The clearest predictions of the cascading trophic interactions hypothesis are that there should be fewer planktivores, more zooplankton and less chlorophyll *a* in more intensely stocked lakes. Furthermore, the abundance of organisms at any given trophic level should covary inversely with the abundance of their predators after controlling for total phosphorus (Fig. 2, top). Since predation is usually size-selective, one should also observe smaller zooplankton when predation by planktivores is intense (Brooks and Dodson 1965) and larger, inedible phytoplankton when zooplankton predation is intense (Vanni 1987) (Fig. 2, bottom). It has also been suggested that the size structure of predator assemblages influences the size and abundance of their prey (Pace 1984, Stein et al. 1988). Although the theoretical bases for predictions on this point are not always clear, I also examine these empirical relationships.

Third, we test the hypothesis that the species of piscivorous fish stocked in a system determines the extent to which top-down type trophic interactions occur. This will be tested by comparing how measures of trophic level biomass and size structure covary with piscivorous fish species stocked. I can then determine the extent to which top-down trophic interactions are dependent on the species of predator being manipulated. The prediction from this hypothesis is that species with very different life history traits and habitat preferences (e.g. lake trout versus walleye) will covary with their resources in different manners after adjusting for trophic status.

Methods

Study Area

To test the effect of piscivorous fish stocking intensity (defined here as the total number of fish stocked in the 6 years prior to sampling, divided by lake surface area) on the biomass and size structure of the phytoplankton, zooplankton and planktivorous fish communities, we selected 24 stocked and 7 non-stocked lakes in southeastern Ontario (Fig. 3). The 31 lakes are located on Precambrian bedrock of the Canadian Shield. The 24 stocked lakes were chosen to include as much variability in numbers and species of fish stocked as possible (Table 1). The 7 non-stocked lakes all contained piscivorous fish and were selected to resemble the stocked lakes geographically and morphometrically while having no known history of fish stocking. Stocking intensity per unit surface area varied by 2 orders of magnitude. The lakes fell into 5 categories: lakes with no known history of piscivorous fish stocking (n = 7), lakes stocked with lake trout (n = 7), F1 splake (n = 7), rainbow trout (n = 2), and yellow walleye (n = 8). Lake trout, F1 splake, and rainbow trout were all stocked as yearlings (mean mass 30 g for lake trout and rainbow trout, 40 g for splake), and walleye were stocked as fingerlings (mean weight 1.2 g) for all lakes except Flower Round which was stocked with advanced fingerlings (mean weight 12 g).

Sampling

The 31 lakes were sampled twice in 1993 and once in 1994 during the period of summer stratification (June through September). Secchi depth and depth of the epilimnion near the center of each lake were determined, and temperature and conductivity profiles obtained using a Y.S.I. S-C-T meter. Quadruplicate samples of total phosphorus, chlorophyll *a* and zooplankton were taken and returned to the lab for analysis. During the summer of 1994, the planktivorous fish community was also evaluated.

Samples for total phosphorus and chlorophyll *a* were obtained using a 2.5 cm diameter Tygon tube sampler integrating over the depth of the epilimnion. Whole water samples were analyzed spectrophotometrically for total phosphorus using persulphate digestion and the molybdenum blue method (Menzel and Corwin 1965). Total chlorophyll *a* was determined by filtering aliquots of whole lake water on Whatman GF/F filters. To assess phytoplankton community size structure, whole lake water was sequentially passed through four filters of decreasing pore size, resulting in 4 size fractions: netplankton (gathered on 35 µm Nitex), nanoplankton (12 µm polycarbonate filters), microplankton (2 µm polycarbonate filters) and picoplankton (Whatman GF/F filters). Chlorophyll *a* was extracted over 24 hours in ice-cold 95% ethanol and assayed spectrophotometrically (Ostrofsky and Rigler 1987).

The zooplankton community was sampled using a calibrated (25 l min^{-1}) open diaphragm bilge pump (Pace 1984). An integrated sample was obtained by pumping a minimum of 30 l of water while raising and lowering the pump intake over the top 10 m of the water column, or to within 0.5 m of the bottom for shallow (< 10 m) lakes. Outflow from the pump was passed through a 35 μm Nitex cone net. The zooplankton were then carefully washed into a Nalgene container and immediately preserved in a 4% formalin-sucrose solution (Haney and Hall 1975). For the purposes of enumeration, zooplankton were subsampled according to the beaker method of Van Guelphen et al. (1982). Subsamples were enumerated using a dissecting microscope at 40X magnification with lengths of individual zooplankton being estimated through the use of a microcomputer based calliper system (Sprules et al. 1981). The number of individuals, and their lengths, were tallied separately by genus for cladocera and by family for copepods. Nauplii were not identified to family, and all rotifers were grouped together. Lengths were converted to biomass using published mass-length regressions for each genus (cladocerans), family (copepod), or taxon (nauplii and rotifers) (Dumont et al. 1975, Bottrell et al. 1976). Zooplankton size structure was expressed as the geometric mean of individual body mass of all zooplankton counted in a given subsample from a given lake.

The planktivorous fish community was sampled using a mixture of passive and active gear to maximize catch (Weaver et al. 1993). The passive gear used in this study consisted of 2 littoral zone trap nets (4.5 m lead, 1.2 m X 0.9 m mouth, mesh size 0.63 cm). A 10 m X 1 m beach seine (mesh size 0.5 cm) was our active gear. Sites for seining and trap netting were chosen in areas with gradually sloping littoral zones and with significant macrophyte growth. A total of 5 seine hauls were obtained from 5 distinct areas in each lake. Trap nets were set for 6 hours from approximately 09:00 until 15:00. Fish caught were identified to species, measured for total length, and released. To develop an index of planktivore abundance, we summed fish abundances from seine and trap net hauls to minimize sample gear bias (Hinch et al 1991, Weaver et al. 1993). As a measure of planktivorous fish community size structure, the mean length of all individuals netted from each lake was calculated (Mills et al. 1987). Our index of planktivorous fish abundance and size structure included only those individuals that have been shown to feed (partially or entirely) on zooplankton as indicated by Scott and Crossman (1973). To remove variability associated with the date of sampling, I did not include any young of the year fish since they were only reliably caught by our gear late in our sampling season.

Statistical Methodologies

To test the effects of bottom-up and top-down interactions on subsequent trophic levels, we examined variance components of general linear models. A saturated model of the variance in any dependent variable in this study (which was measured on multiple samples on each of 3 dates) could be expressed as:

$$\begin{aligned}\text{dependent variable variance} = {} & \text{among lake variance} \\ & + \text{seasonal (among-date, within-lake) variance} \\ & + \text{among replicate (within date and lake) variance}\end{aligned} \tag{1}$$

For present purposes, we were only interested in the among-lake variance. Therefore, the variance associated with a categorical LAKE (31 categories) variable in the following model:

$$\begin{aligned}\text{dependent variable} = {} & \text{LAKE} \\ & + \text{residual variance}\end{aligned} \tag{2}$$

served to define the total variance of interest in subsequent models. We then partitioned the LAKE variance into components attributable to independent variables and to residual among-lake variation. Thus, a typical bottom-up multiple regression model of total phosphorus and a dependent variable that was measured 3 times over 2 years would be:

$$\begin{aligned}\text{dependent variable} = {} & \text{total phosphorus} \\ & + \text{LAKE} \\ & + \text{residual variance.}\end{aligned} \tag{3}$$

To test for the significance of the relationship between the dependent variable and total phosphorus, we constructed F statistics by comparing the among-lake variability attributable to total phosphorus added first to the model to the additional among-lake variability attributable to LAKE. The residual variance in model (3) represents the variance among replicate samples gathered on particular dates and among dates; this variance is not relevant to the present comparisons. I used this model in preference to a conventional analysis of variance in order to avoid the problems of non-independence associated with the 3 repeated measures for each lake.

Top-down analyses resembled those described for bottom-up models. In all cases, stocking intensity was used as an independent variable, and a measure of trophic level biomass or size structure was used as the dependent variable. We controlled for variations resulting from differences in trophic status by including total phosphorus concentration as a linear covariate in all models. Thus, a typical multiple regression model of piscivorous fish stocking intensity and a dependent variable would be:

dependent variable = total phosphorus (4)
+ piscivorous fish stocking intensity
+ LAKE
+ residual variance

We calculated the F statistic as the ratio of the mean square for piscivorous fish stocking intensity (added as the penultimate variable in the model) to the within-lake variability attributable to LAKE (added as the last variable).

To test for top-down effects on chlorophyll *a* size structure, we used the following analysis of covariance:

chlorophyll *a* = total phosphorus (5)
+ SIZE
+ top-down variable
+ SIZE * top-down variable
+ LAKE
+ residual variance

where SIZE is a categorical variable distinguishing four size fractions (>35 μm, 12 - 35 μm, 2 - 12 μm, and < 2 μm). The top-down independent variables included in this analysis were piscivorous fish stocking intensity, planktivorous fish abundance, mean individual planktivorous fish length, zooplankton biomass, and mean individual zooplankton dry mass. The interaction term tests the hypothesis that the distribution of chlorophyll *a* among size fraction depends upon the independent variable.

To test for differential top-down effects incurred by the four different species of sport fish that were stocked we carried out the following analysis of covariance:

$$\begin{aligned}\text{dependent variable} = {} & \text{total phosphorus} \\ & + \text{piscivorous sport fish stocking intensity} \\ & + \text{SPECIES} \\ & + \text{piscivorous sport fish stocking intensity} * \text{SPECIES} \\ & + \text{LAKE} \\ & + \text{residual variance}\end{aligned} \tag{6}$$

where SPECIES is a categorical variable distinguishing from species the species stocked (lake trout, splake, rainbow trout, walleye, and non-stocked lakes). Dependent variables were chlorophyll *a*, zooplankton biomass, mean individual zooplankton dry mass, planktivorous fish abundance, and mean individual planktivorous fish length.

Results

Trophic status of the lakes ranged from oligotrophic (TP = 3.7 $\mu g\ l^{-1}$) to mesotrophic (TP = 23.7 $\mu g\ l^{-1}$). The among-lake variation in morphometric, chemical and biological characteristics was high (Table 1). All lakes in the study except one (Joe's, maximum depth 4.3 m) were stratified when sampled.

Bottom-Up Relationships

Of the variables included in the bottom-up analysis, only those at the phytoplankton and zooplankton levels were found to be significant (Fig. 4). Chlorophyll *a* was strongly and positively related to total phosphorus (eqn. 7, Table 2 and Fig. 5) as predicted by the bottom-up models. The relationship between zooplankton biomass and total phosphorus was also nearly significant with a trend towards increased zooplankton biomass with increasing total phosphorus ($r = 0.33$, $n = 93$, $P = 0.07$). Highly significant inverse relationships between mean individual zooplankton dry mass and total phosphorus (eqn. 8, Table 2 and Fig. 6A) and mean individual zooplankton dry weight and chlorophyll *a* (eqn. 9, Table 2 and Fig. 6B) were found. Thus, nutrient-rich lakes have increased amounts of chlorophyll *a* and zooplankton communities dominated by smaller bodied individuals. No significant relationships were found between planktivorous fish abundance or size structure and their resources ($P > 0.05$).

Top-down relationships

In no case could we detect an effect of piscivorous fish stocking intensity on any other trophic level after controlling for total phosphorus (Fig. 7). Planktivorous fish abundance is nearly significantly related to piscivore stocking intensity ($r= 0.10$, $n = 31$, $P = 0.14$) (Fig. 8A), and if we remove the non-stocked lakes from the data set, we obtain a significant relationship ($r = 0.46$, $n=24$, $P=0.03$) (eqn. 10, Table 3). However, the top-down hypothesis predicts that increased stocking intensity should lead to fewer planktivores, whereas we observe the opposite! Piscivore stocking intensity explained no significant residual variation in zooplankton biomass (Fig. 9A), chlorophyll *a* concentration (Fig. 9C) or the size structure of planktivorous fish (Fig. 8B), zooplankton (Fig. 9B) or phytoplankton (Table 4, section v).

The trophic interaction where top-down effects were most clearly evident was at the zooplankton-phytoplankon link (Fig. 7). Chlorophyll *a* concentration is weakly negatively correlated with zooplankton biomass after controlling for total phosphorus (eqn. 11, Table 3 and Fig 10A). It is also negatively related to mean zooplankton size (eqn. 12, Table 3 and Fig. 10B). Both of these observations are consistent with the predictions of the top-down hypothesis (Fig. 2). The size structure of chlorophyll *a* does not depend upon zooplankton biomass (Table 4, i). It may depend upon mean individual zooplankton dry mass (Table 4, ii), but the significance is marginal.

A weaker top-down effect is evident between planktivorous fish and zooplankton. Although zooplankton *biomass* does not decline with planktivore abundance as top-down hypotheses would predict ($r = 0.02$, $n=31$, $P=0.90$), zooplankton *abundance* is strikingly lower in lakes with more abundant planktivores (eqn. 13, Table 3 and Fig. 11). There is no clear effect of planktivorous fish on zooplankton size ($P = 0.16$).

Although overall stocking intensity (without regard to the species involved) was not a significant factor in the top-down analyses, chlorophyll *a* and zooplankton size structure do depend on the particular species of piscivorous sport fish stocked (Table 5 i, iii, and Fig. 12). Analyses of covariance are equally consistent with the hypotheses that the means of these parameters depend upon the species of piscivore stocked (Table 5 i, iii, and Fig. 12), or that the interaction of these parameters with stocking intensity depends upon the species stocked (not shown). In general, there was significantly less chlorophyll *a* (Tukey test $P < 0.05$), and a trend towards larger-bodied zooplankton in lakes stocked with rainbow trout than in the other four lake categories after adjusting for total phosphorus as a linear covariate (Fig. 12). No significant relationships were observed between zooplankton biomass, planktivorous fish abundance, or mean individual planktivorous fish length and the species of piscivorous sport fish stocked (Table 5 ii, iv, and v. respectively).

Discussion

Bottom-Up Relationships:

Our bottom-up results are very similar to other analogous relationships in the literature. Both chlorophyll *a* and zooplankton biomass increases with total phosphorus, as has been found elsewhere (Dillon and Rigler 1974, Yan 1986). The literature is equivocal about the exact effect of trophic status on zooplankton. For example, some studies have shown a stronger positive relationship between zooplankton biomass and chlorophyll *a* than between zooplankton and phosphorus (McCauley and Kalff 1981, Bays and Crisman 1983), while others find the reverse (Yan 1986). In some studies, mean individual zooplankton dry mass is more strongly related to total phosphorus than is zooplankton biomass (e.g. the present work), whereas others find the opposite (Pace 1986). Although the way in which resources affect the zooplankton appears to vary among regions (we will explore this question further elsewhere), some effect of resources on zooplankton is nearly always observed (Bays and Crisman 1983, Richman and Sager 1990). The lack of relationships between characteristics of the planktivorous fish assemblage and resources in our study is consistent with the hypothesis of McQueen et al.

(1986) that bottom-up relationships are strongest at the bottom of the food web and dissipate rapidly (becoming non-significant) as one moves up trophic levels.

The relevance of the bottom-up results are two fold. First, the highly significant relationships with total phosphorus indicate that the lake systems we studied are probably nutrient-limited, and that it is reasonable to control for trophic status before testing for top-down effects. Second, the results indicate that the lakes included in this study are not anomalous with respect to other lake systems. Our results are essentially consistent with the predictions (Fig. 1) of the bottom-up hypothesis of resource control of biomass and size structure at the bottom of the food web (i.e. total phosphorus, chlorophyll *a*, and zooplankton) (Fig. 4).

Top-Down Relationships:

Zooplankton

Chlorophyll *a* concentration was found to depend upon both zooplankton biomass and mean individual zooplankton dry mass after adjusting for total phosphorus: there is less chlorophyll *a* when zooplankton are large and abundant. Thus, we find clear top-down effects of zooplankton on phytoplankton. Moreover, our results resemble others that have related a portion of the residual variability in the chlorophyll *a* - total phosphorus relationship to zooplankton community structure (Pace 1984, Quirós 1990, Mazumder 1994). However the amount of residual variability in chlorophyll *a* explained by zooplankton biomass ($r^2 = 0.12$) and mean individual dry weight ($r^2 = 0.23$) in the top-down models is 1/5 and 1/3 respectively that explained by total phosphorus ($r^2 = 0.61$)

in the bottom-up model. This indicates that resources (bottom-up processes) are much more important than predators (top-down processes) in regulating what we observe at the level of the phytoplankton.

Planktivorous Fish

Planktivorous fish abundance and size structure were found to have little or no top-down impact on their resources contrary to our predictions (Fig. 2). Similar results from a survey of 97 Argentinean lakes are presented by Quirós (1990). As was found in this study, there was no relationship between the frequency of planktivorous fish and macrozooplankton biomass. In another multi-lake study, Persson et al. (1992) compared 11 Swedish lakes examining the effects of food chain length on trophic level biomass. Results from the lakes containing piscivorous sport fish were found to be similar to our results in that no relationships were found between planktivore abundance and zooplankton or chlorophyll *a*.

Contrary to zooplankton biomass, zooplankton abundance (number of organisms l^{-1}) was found to be highly significantly related to planktivorous fish abundance after adjusting for total phosphorus. This result has been shown for both whole-lake (Lafontaine and McQueen 1991) and enclosure (Hambright et al. 1986) studies. The inverse relationship between zooplankton and planktivore abundance may be coupled with a shift in zooplankton size structure (Brooks and Dodson 1965). There was no detectable effect of planktivores on zooplankton size as Auclair et al. (1993) found in a similar set of Canadian shield lakes. Once again, top-down effects are very weak.

In only one case was a prediction of the cascading trophic interactions hypothesis (Fig. 2) supported by our results at the level of the planktivorous fish (Fig. 7). This is not because the trophic cascade is uncoupled at some link, as suggested by McQueen and Post (1988). In this study, we found subtle top-down effects at every link between the planktivores and chlorophyll *a*, indicating that trophic interactions are not so much uncoupled, as they fail to propagate down more than one level.

One possible concern in this study is that we sampled the pelagic plankton community and related it to the littoral zone fish community. It is possible that the littoral zone fish community is unable to exploit resources in the pelagic zone (France 1995). If this were so it could explain the non-significant results observed. However one would expect that in smaller lakes the pelagic and littoral areas would (due to their proximity) be more tightly linked. Thus littoral zone fishes in smaller lakes would be more efficient at exploiting the pelagic zone. However, if pelagic and littoral processes were partly uncoupled in our study, lake surface area should be related to plankton - fish relationships. We found that adding surface area does not significantly improve these relationships.

Stocking Intensity:

The clearest result of this study is that, after adjusting for log total phosphorus as a linear covariate, overall stocking intensity (measured as the total number of piscivorous fish, without respect to species stocked in the 6 years prior to sampling, divided by lake surface area) had no detectable impact on anything (Fig. 7). We had predicted that we would observe a decrease in planktivorous fish abundance with a shift towards larger individuals, an increase in zooplankton biomass and body size, and a decrease in chlorophyll *a* with a shift towards larger (>35 μm) less edible size fractions in response to increased stocking intensity (Fig. 2). Thus with no results confirming our predictions we must reject the hypothesis that along a gradient in stocking intensity (at least as carried out by the Ontario Ministry of Natural Resources) we should observe gradients in abundance and size structure of the planktivorous fish, zooplankton, and phytoplankton communities.

However, we do detect a weak effect of stocking intensity if we consider the species of piscivore stocked. In general, after adjusting for total phosphorus, lakes stocked with rainbow trout tended to have larger-bodied zooplankton and less chlorophyll *a* than the four other categories of lake. Thus, for the subset of lakes stocked with rainbow trout, we have results confirming the predictions of the top-down trophic cascade model (Fig. 2). Similar results for a rainbow trout stocked lake are reported by Elser et al. (1995). Whereas the purpose of this study was to examine the impact of increased piscivorous sport fish densities on lower trophic levels, Elser et al. (1995) examined the response of lower trophic levels to artificially decreased rainbow trout densities. In Castle Lake, long-term rainbow trout stocking was halted and the response of the aquatic community monitored over a 3 year period. It was found that zooplankton body size decreased, and primary production increased after the cessation of rainbow trout stocking (Elser et al 1995). This is consistent with our results. However, in contrast to Elser et al. (1995), we detected no effect of rainbow trout stocking on the planktivorous fish assemblage, which raises the question of how top-down effects can skip trophic levels. This could be due to the omnivorous nature of this species of trout. Elser et al. (1995)

found that the stocked rainbow trout in Castle Lake were feeding almost exclusively on larger benthic and pelagic invertebrates (e.g. *Chaoborus* larvae). If invertebrate predators have a much larger impact than do planktivorous fish, and if rainbow trout have a particularly strong impact on the invertebrates, then the zooplankton could be freed from predation, irrespective of the planktivorous fish community.

In principal, failure to detect significant relationships between overall stocking intensity (without respect to species stocked) and our measures of trophic level biomass and size structure could be due to low statistical power (Peterman 1990). However, given our experimental design, we required a treatment effect of only $r^2 = 0.08$ to detect a significant relationship. Thus if relationships between stocking intensity and our measures of trophic level biomass and community size structure actually exist, they can not explain more than 8% of the variation in the dependent variable.

Our results are consistent with the Lake Ontario experience of large scale salmonid stocking. Lake Ontario has been intensely stocked with salmonid fishes over the last 30 years, leading to an increase in sport fish numbers (Christie et al. 1987). However, long-term records of pelagic planktivorous fish abundance and zooplankton biomass and size structure indicate no substantial change attributable to salmonid stocking (Lean et al. 1990, Mazumder et al. 1992). Chlorophyll *a* concentrations have decreased in recent years, but the decrease is entirely attributable to decreases in phosphorus availability in the system (Lean et al. 1990).

Although evidence from Lake Ontario suggests that stocking with piscivorous sport fish has little or no impact on the lower trophic levels in the pelagic community, other studies have shown the opposite. Mills et al. (1987) demonstrated that by establishing a predatory fish community in Canadarago Lake they could affect the panfish and zooplankton communities. After 5 years of stocking walleye and muskellunge the predator community had doubled, planktivorous fish length increased, abundance decreased, and zooplankton shifted to a larger, *Daphnia* dominated community. Impacts on the planktivorous fish community through stocking with predacious fish have recently been reported by Prejs et al. (1994). In response to stocking with northern pike, the size structure of the planktivorous fish community was shifted to larger bodied, less vulnerable to predation, size / year classes. Shapiro and Wright (1984) and Carpenter et al. (1987) were also able to greatly affect the aquatic communities by stocking with a high ratio of piscivorous to planktivorous fishes. Zooplankton became dominated by large filter feeding *Daphnia* species and chlorophyll *a* was lowered substantially.

The greatest difference between our study lakes, Lake Ontario, and the examples cited above are lake size. Studies showing significant trophic cascades are generally quite small (Prejs et al. (1994): volume 2.0 X 10^5 m^3; Shapiro and Wright (1984): volume 3.6 X 10^5 m^3; Carpenter et al. (1987): volume 8.3 X 10^4 m^3). In contrast the lakes in this study and those that had similar results to ours are much larger (this study: range in volume 1.2 X 10^5 m^3 - 6.9 X 10^8 m^3; Quirós (1990): mean volume 1.8 X 10^8 m^3; Persson et al. (1992): range in surface area (volume not available) 90 Ha - 5400 Ha, range in maximum depth 22 m - 48 m). It has been shown that top-down type trophic dynamics and trophic interactions are much more strong in shallow, small lake systems (Moss et al. 1994, Reynolds 1994).

A recent study by Qin and Culver (1995) demonstrates the potentially confounding influence of ontogenic diet shifts in the use of sport fish stocking as a manipulation of the aquatic food web. The authors conclude that stocking young-of-the-year sport fish with the intent of initiating a trophic cascade can backfire in that the stocked fish are still in the planktivorous stage of their lifecycle. In this situation one is effectively supplementing the planktivorous rather than piscivorous fish community. If this were occurring in the lakes sampled in this study however, it leads to the prediction that we would observe a relationship opposite to the one predicted for stocking intensity on zooplankton biomass and size structure. However, we do not obtain such a result when we look at the relationship between zooplankton biomass (Fig. 9A), or size structure (Fig. 9B) and stocking intensity.

It is also possible that we did not detect significant stocking intensity effects because sport fish stocking is ineffective. We assume that stocking predacious fishes does increase piscivorous fish density. If, in fact, stocked fish do not survive long enough to significantly impact their resources, then they could not induce a trophic cascade capable of altering the biomass or size structure of their prey. However, work carried out on the walleye lakes in this study indicate that stocked individuals were surviving, and constituted between 16 % and 60 % of the adult walleye population (Seip 1995). It is also possible that the level of stocking carried out by the Ontario Ministry of Natural Resources is insufficient to trigger a trophic cascade. Lazzaro et al. (1992) suggest that, for planktivorous fish to impact phytoplankton, their biomass must be reduced below a critical level of 10 g m^{-3}. Carpenter (1989) hypothesized that a 10-fold increase in piscivorous fish biomass is necessary for a trophic cascade to impact the phytoplankton community. However, we do not have data on piscivore biomass pre- and post-stocking and as such, cannot compare Carpenter's (1989) suggested manipulation strength to that of the lakes in this study.

The implications of these results are that cascading trophic interactions appear to be largely unimportant in medium sized and large, oligotrophic to mesotrophic lakes stocked annually with young of the year piscivorous sport fish. Though we observed an effect of the species of piscivore stocked on the zooplankton and phytoplankton, we were unable to explain any of the among lake variation in trophic level biomass or size structure by arranging lakes along a gradient of piscivorous sport fish manipulation. This indicates that the trophic cascades demonstrated in the literature may be dependent on both the species of fish manipulated and the size of the system (small lake, pond, or enclosure) in which they are carried out. From a biomanipulation standpoint, piscivorous fish stocking has been advocated as a method of bringing about lower chlorophyll *a* concentrations and greater water clarity (Benndorf 1984). More recently however, it has been suggested that for this practice to be successful it must be coupled with decreases in phosphorus loading (Benndorf 1987, 1990). When we consider the case of Lake Ontario we see that reduced phosphorus loading was almost entirely responsible for the decreased chlorophyll *a* and increased water clarity, whereas stocking with predacious sport fish has had little or no impact on the aquatic community (Lean et al. 1990). Reynolds (1994) suggests that coupling biomanipulation with decreasing phosphorus loading defeats the integral purpose of biomanipulation as it was proposed as a management technique to decrease chlorophyll *a* and phytoplankton biomass irrespective of nutrient load (Shapiro 1995).

Conclusion

This study was undertaken to better understand how biomass and size structure in aquatic system are mediated. From examining various aspects of resource limitation (bottom-up) and consumer control (top-down) models we have demonstrated that resources (in particular total phosphorus) are much more important than predators in structuring the biomass and size structure of trophic levels. Second, we found that significant food web interactions were limited to the phytoplankton and zooplankton, becoming non-significant at the planktivorous fish level. Piscivorous sport fish stocking as a manipulation of the food web had little or no measurable impact on the among-lake variation in planktivorous fish, zooplankton, or phytoplankton abundance, biomass, or size structure. We did observe an effect of the species of piscivore stocked on zooplankton and phytoplankton, yet there remains little evidence supporting the hypothesis that manipulations of the top predators in a lake system can cascade down the food web, altering biomass and size structure of all subsequent trophic levels. Furthermore, the results found here suggest that as a management tool for controlling nuisance phytoplankton, manipulations of top predators should be avoided in light of nutrient reductions which we have found to be much more important in regulating phytoplankton communities. Future work should focus on the roles of mean depth, lake volume, and different piscivorous sport fish species in determining the outcome of cascading trophic interactions.

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Table 1. The median and range of morphometric and limnological variables of the 31 lakes analyzed for this study.

variable	acronym	median	minimum	maximum
surface area (ha)		106	10.1	1590
mean depth (m)		9.2	1.2	43.1
maximum depth (m)		25.9	4.3	145
pH		8.3	7.5	8.8
mean epilimnetic conductivity (µmhos cm^{-2})		204	77.5	390
secchi depth (m)		5.4	2.5	8.6
total phosphorus concentration (µg l^{-1})	TP	8.3	3.7	23.7
chlorophyll *a* concentration (µg l^{-1})	Chl *a*	2.4	0.8	10.7
zooplankton biomass (µg dry mass l^{-1})	ZBM	117	25.7	542
zooplankton density (number l^{-1})	ZDENS	124	35.4	686
mean individual zooplankton dry mass (µg individual^{-1})	MZDM	0.22	0.06	1.01
planktivorous fish abundance (catch per unit effort)	PLF	96	1	1600
mean individual planktivorous fish length (cm)	MPLF	6.9	4	9.1
piscivorous fish stocking intensity (total number of fish stocked in 6 years prior to study Ha^{-1})	PIFSI	273	34	1380

Table 2. Summary of significant regression models for bottom-up relationships for both biomass and size structure. (Units and acronyms are listed in Table 1).

equation	model	r	P
(7)	$\log(\mathrm{Chl}\ a) = 0.97 \log(\mathrm{TP}) - 0.52$	0.78	<0.001
(8)	$\log(\mathrm{MZDM}) = -0.55 \log(\mathrm{TP}) - 0.15$	-0.49	0.004
(9)	$\log(\mathrm{MZDM}) = -0.62 \log(\mathrm{Chl}\ a) + 0.42$	-0.62	<0.001

Table 3. Summary of significant regression models for top-down relationships for abundance, biomass, and size structure adjusted using log total phosphorus as a linear covariate. (Units and acronyms are listed in Table 1).

equation	model	r	P
(10)	log (PLF) = 0.67 log (PIFSI) - 0.17*	0.46	0.03
(11)	log (Chl *a*) = - 0.18 log (ZBM) - 0.00	-0.35	0.06
(12)	log (Chl *a*) = -0.33 log (MZDM) - 0.00	-0.48	0.01
(13)	log (ZDENS) = - 0.18 log (PLF) - 0.00	-0.64	<0.001

* non-stocked lakes removed from model

Table 4. Analysis of covariance results examining the effects of total phosphorus (TP), zooplankton biomass (ZBM), mean individual zooplankton dry mass (MZDM), planktivorous fish abundance (PLF), mean individual planktivorous fish length (MPLF), and piscivorous fish stocking intensity (PIFSI) on chlorophyll *a* size structure. (Units are listed in Table 1). Chlorophyll *a* size fractions are: > 35µm, 12µm - 35µm, 2µm - 12 µm, and < 2 µm.

i. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	8.8	53.99	<0.001
log (ZBM)	0.44	2.69	0.11
size fraction	0.53	1.09	0.37
log (ZBM)*size fraction	0.24	0.49	0.7
error	4.88		

ii. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	4.91	35.32	<0.001
log (MZDM)	1.17	8.45	0.01
size fraction	0.98	2.35	0.09
log (MZDM)*size fraction	1.11	2.63	0.07
error	4.17		

Table 4. Continued

iii. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	2.12	32.72	<0.001
log (PLF)	<0.01	0.05	0.82
size fraction	0.32	1.62	0.19
log (PLF)*size fraction	0.05	0.27	0.85
error	7.44		

iv. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	2.23	35.77	<0.001
log (MPLF)	0.11	1.72	0.19
size fraction	0.32	1.71	0.17
log (MPLF)*size fraction	0.21	1.11	0.35
error	7.18		

v. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	8.36	46.7	<0.001
log (PIFSI)	<0.01	0.01	0.94
size fraction	0.59	1.10	0.36
log (PIFSI)*size fraction	0.11	0.19	0.9
error	5.37		

Table 5. Analysis of covariance results examining the effects of total phosphorus, piscivorous sport fish stocking intensity, and sport fish species stocked (categorical) on chlorophyll *a*, zooplankton biomass, mean individual zooplankton dry mass, planktivorous fish abundance, and mean individual planktivorous fish length. Higher order interactions were not significant in these models, and they are not included here. (Units are listed in Table 1).

i. dependent variable: log (chlorophyll *a*)

source	S.S.	F-ratio	P
log (TP)	1.08	39.53	<0.001
log (PIFSI)	0.01	0.29	0.59
SPECIES	0.4	3.69	0.02
error	0.71		

ii. dependent variable: log (zooplankton biomass)

source	S.S.	F-ratio	P
log (TP)	0.37	3.84	0.06
log (PIFSI)	0.01	0.15	0.7
SPECIES	0.25	0.65	0.63
error	2.48		

Table 5. Continued

iii. dependant variable: log (mean individual zooplankton dry mass)

source	S.S.	F-ratio	P
log (TP)	0.26	4.56	0.04
log (PIFSI)	0.01	0.12	0.73
SPECIES	0.72	3.2	0.03
error	1.47		

iv. dependent variable: log (planktivorous fish abundance)

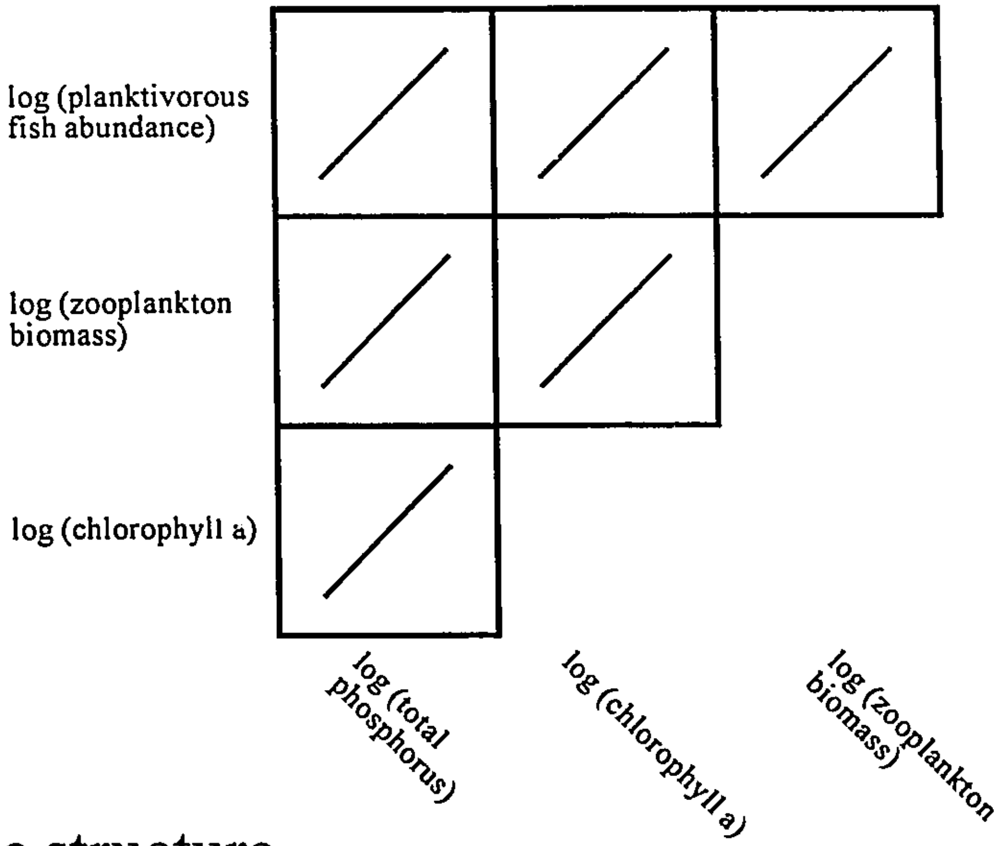
source	S.S.	F-ratio	P
log (TP)	0.01	0.02	0.89
log (PIFSI)	1.26	2.61	0.12
SPECIES	2.79	1.45	0.25
error	11.59		

v. dependant variable: log (mean individual planktivorous fish length)

source	S.S.	F-ratio	P
log (TP)	<0.01	0.17	0.69
log (PIFSI)	0.01	2.34	0.14
SPECIES	0.46	2.15	0.11
error	0.13		

Figure 1. Schematic representation of the predictions of the bottom-up model of resource limitation for trophic level biomass and size structure as they pertain to lakes differing in piscivorous fish stocking intensity.

Biomass.



Size structure.

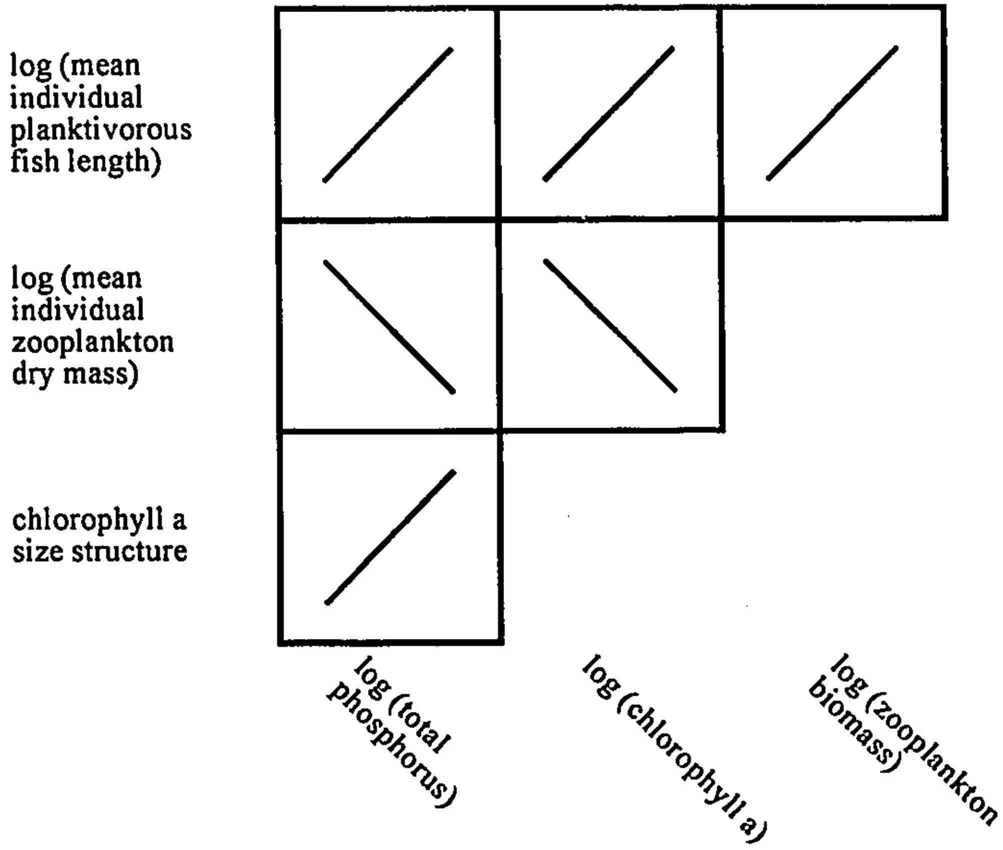
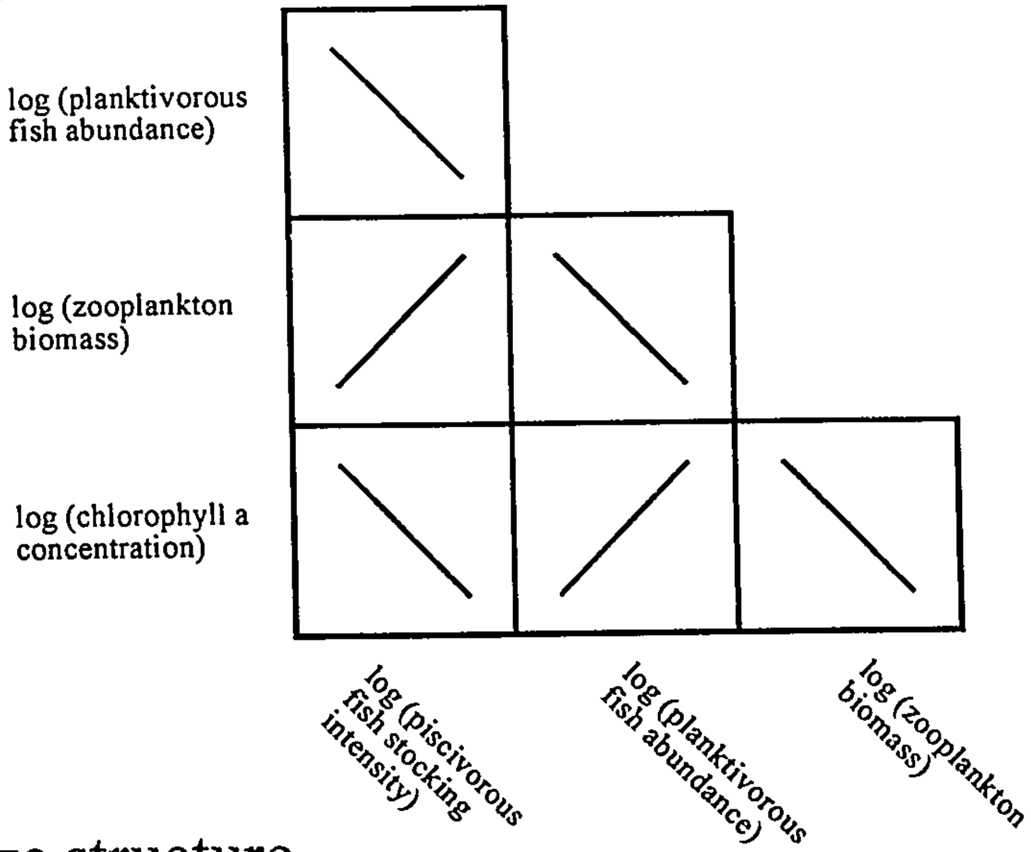


Figure 2. Schematic representation of the predictions of the cascading trophic interactions hypothesis for trophic level biomass and abundance, and size structure as they apply to a series of lakes differing in piscivorous fish stocking intensity.

Biomass.



Size structure.

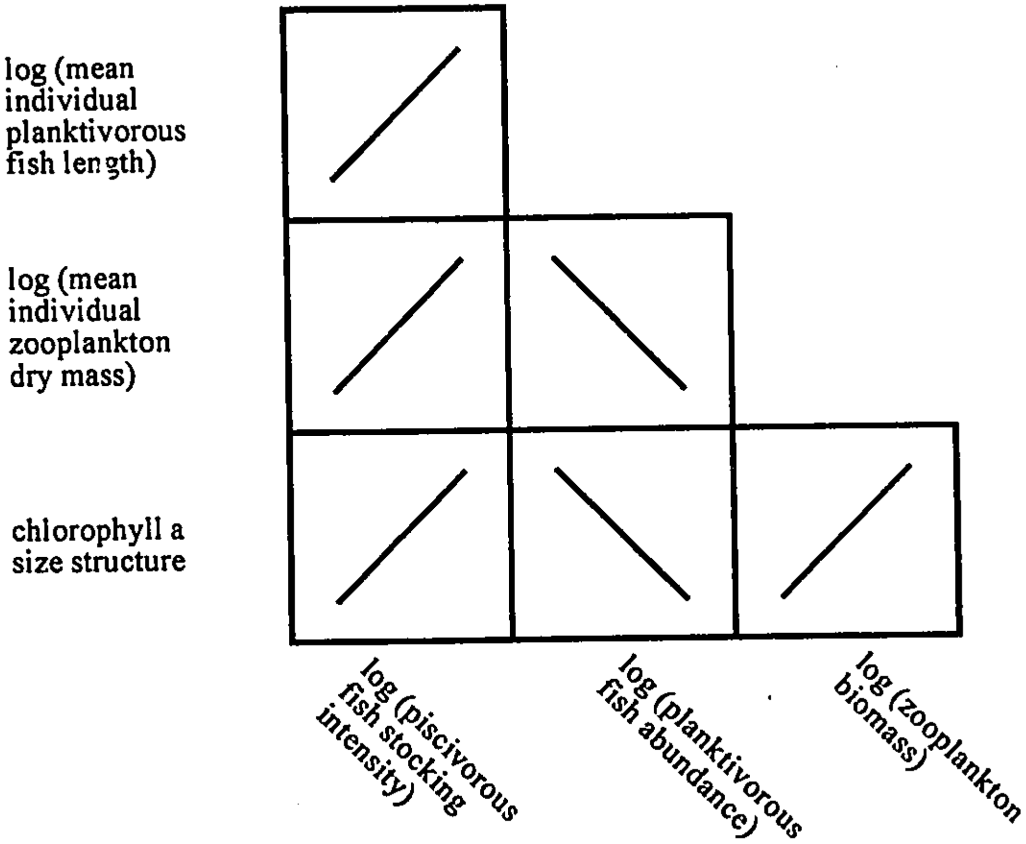


Figure 3. Location of 31 sampling sites in southeastern Ontario, Canada.

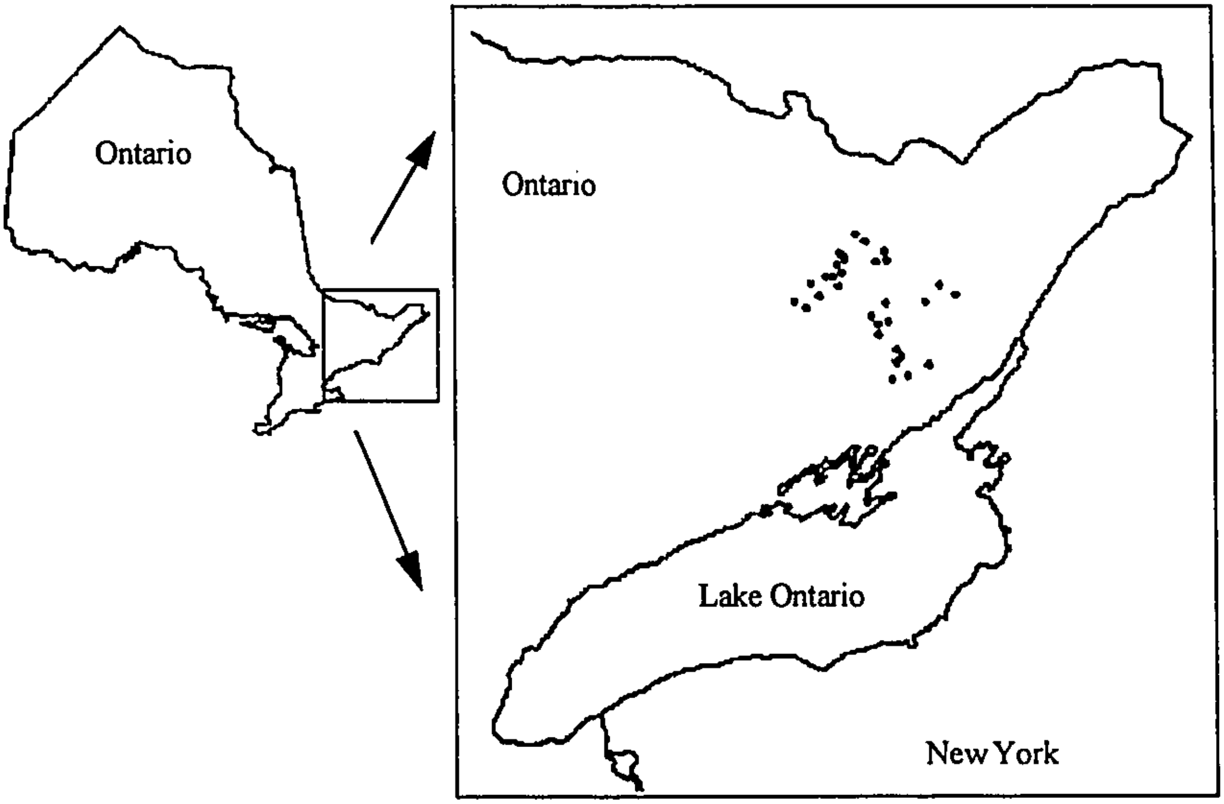
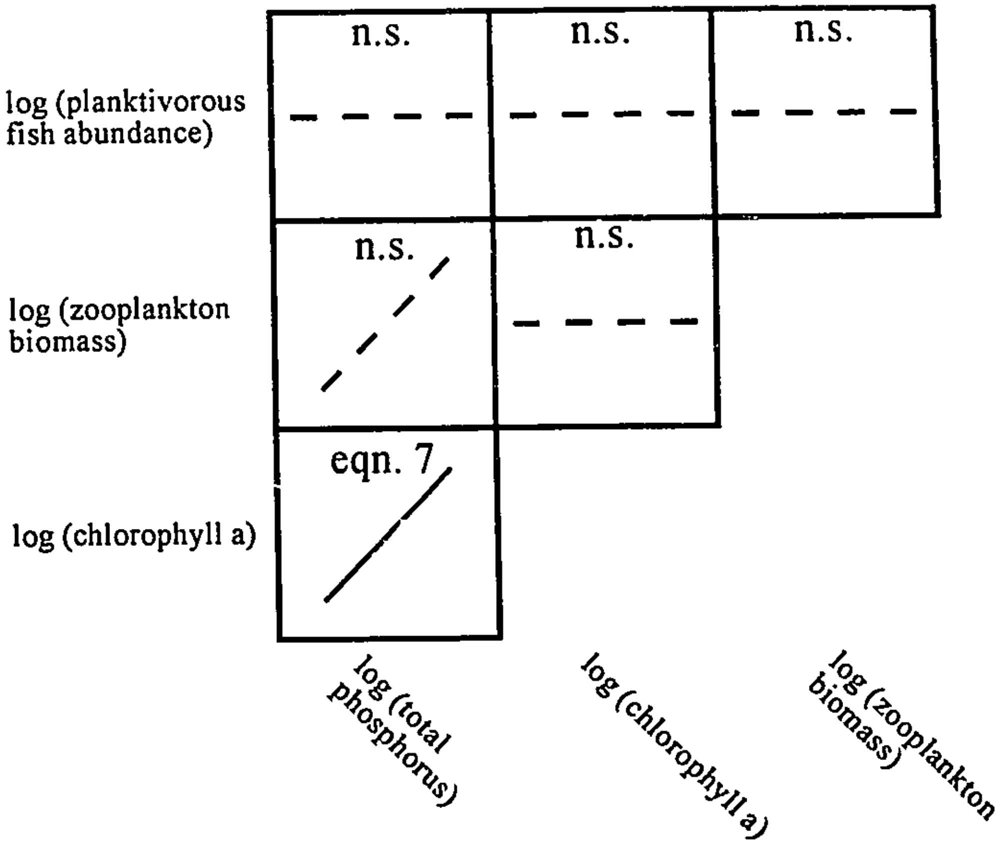

Ontario
Ontario
Lake Ontario
New York

Figure 4. Schematic representation of the results for the bottom-up model of resource limitation for trophic level biomass and abundance, and size structure as they apply to a series of lakes differing in piscivorous fish stocking intensity. Dashed horizontal lines represent non-significant relationships. Solid lines with non-zero slope indicate significant relationships (equations listed in Table 2). Dashed lines with non-zero slope represent near-significant relationships ($0.05 < P < 0.15$).

Biomass.



Size structure.

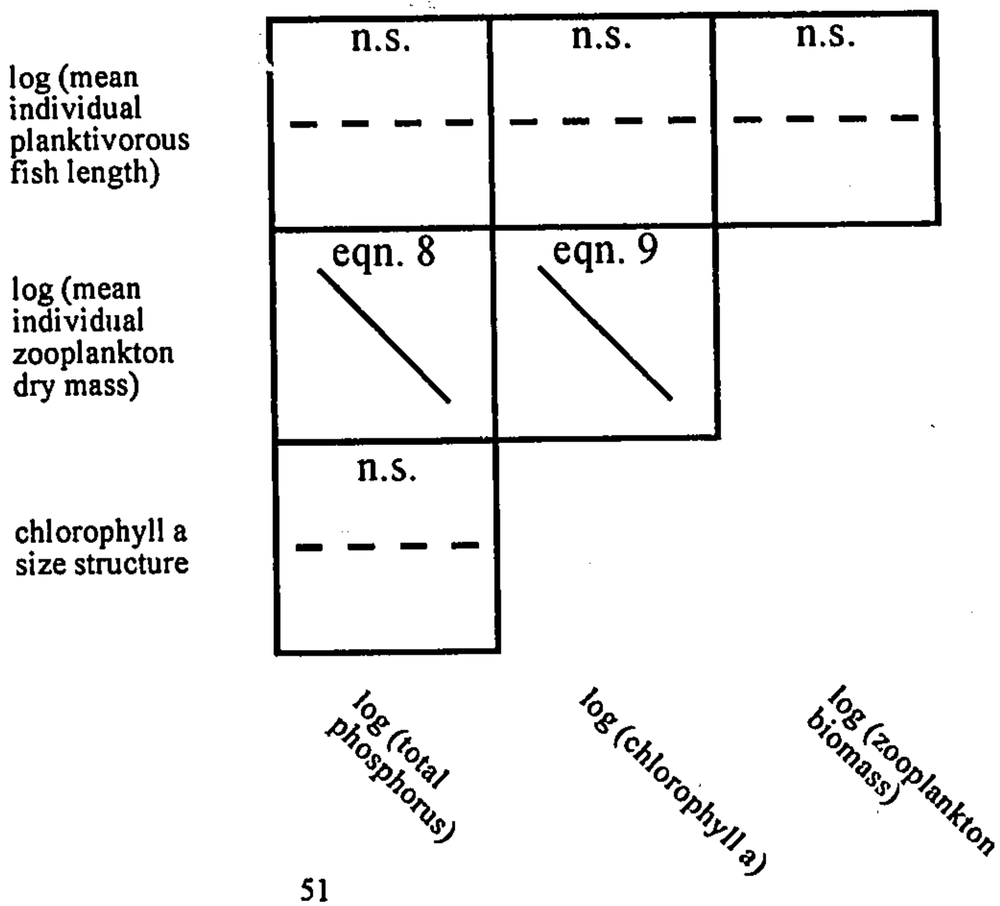


Figure 5. The relationship between log chlorophyll *a* and log total phosphorus ($r^2 = 0.61$, $n = 31$, $P < 0.001$).

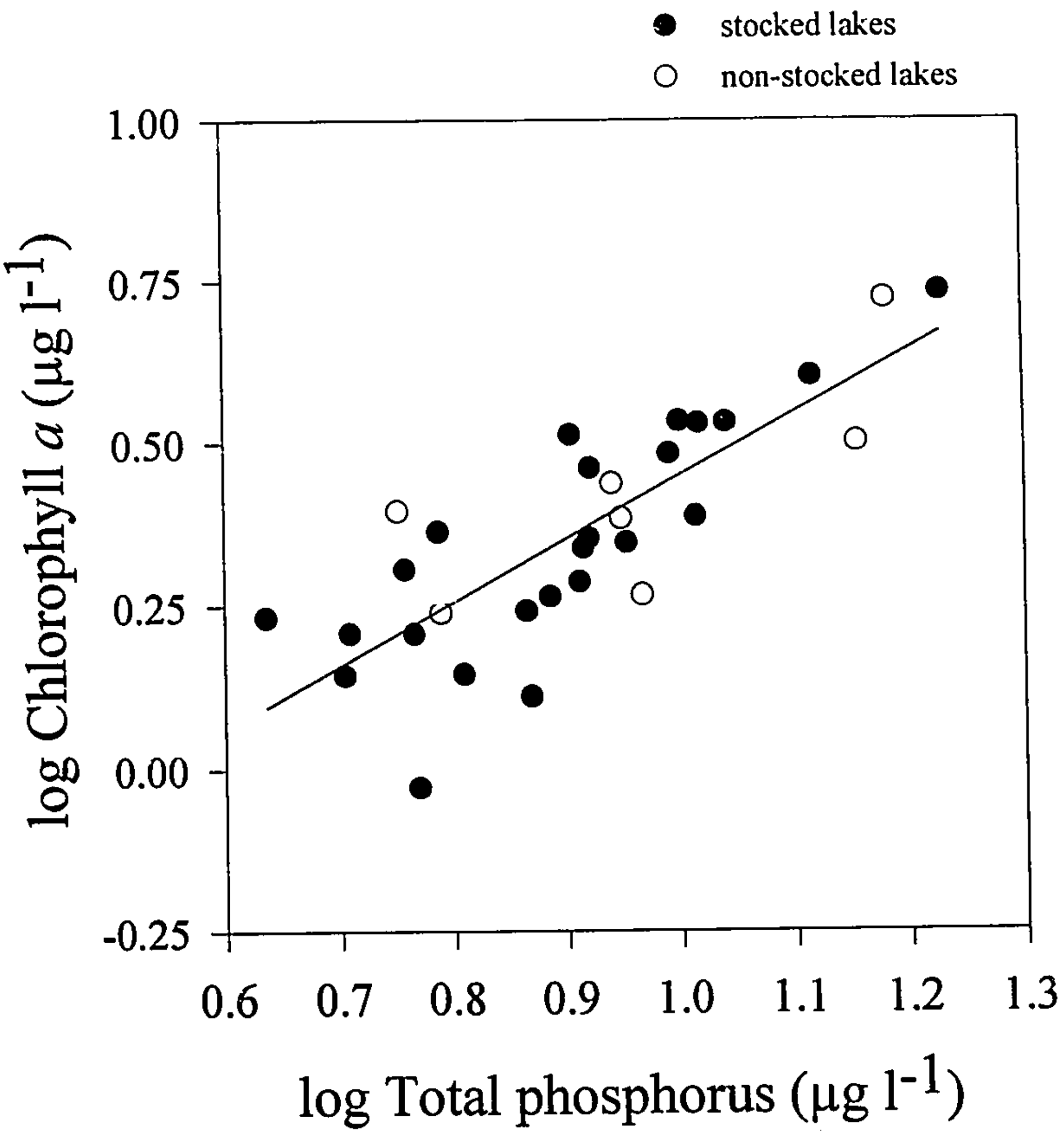

● stocked lakes
○ non-stocked lakes
1.00
0.75
0.50
0.25
0.00
-0.25
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
log Chlorophyll *a* (μg l^{-1})
log Total phosphorus (μg l^{-1})

Figure 6. The relationships between: A. log mean individual zooplankton dry mass and log total phosphorus ($r^2 = 0.24$, $n = 31$, $P = 0.004$); and B. log mean individual zooplankton dry mass and log chlorophyll *a* ($r^2 = 0.39$, $n = 31$, $P < 0.001$). The equations describing these relationships are given in Table 2. Filled circles represent lakes stocked with piscivorous sport fish, open circles represent non-stocked lakes.

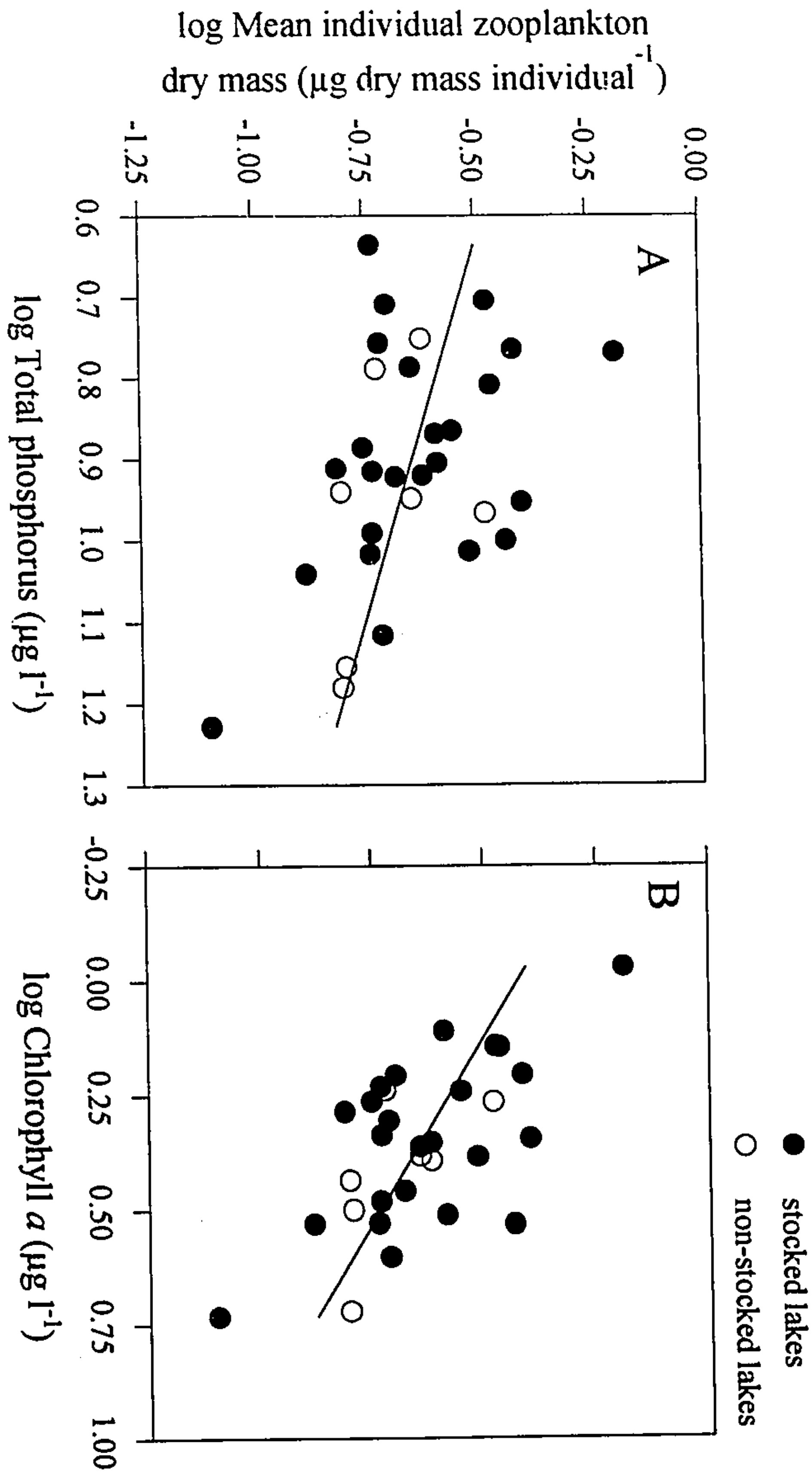
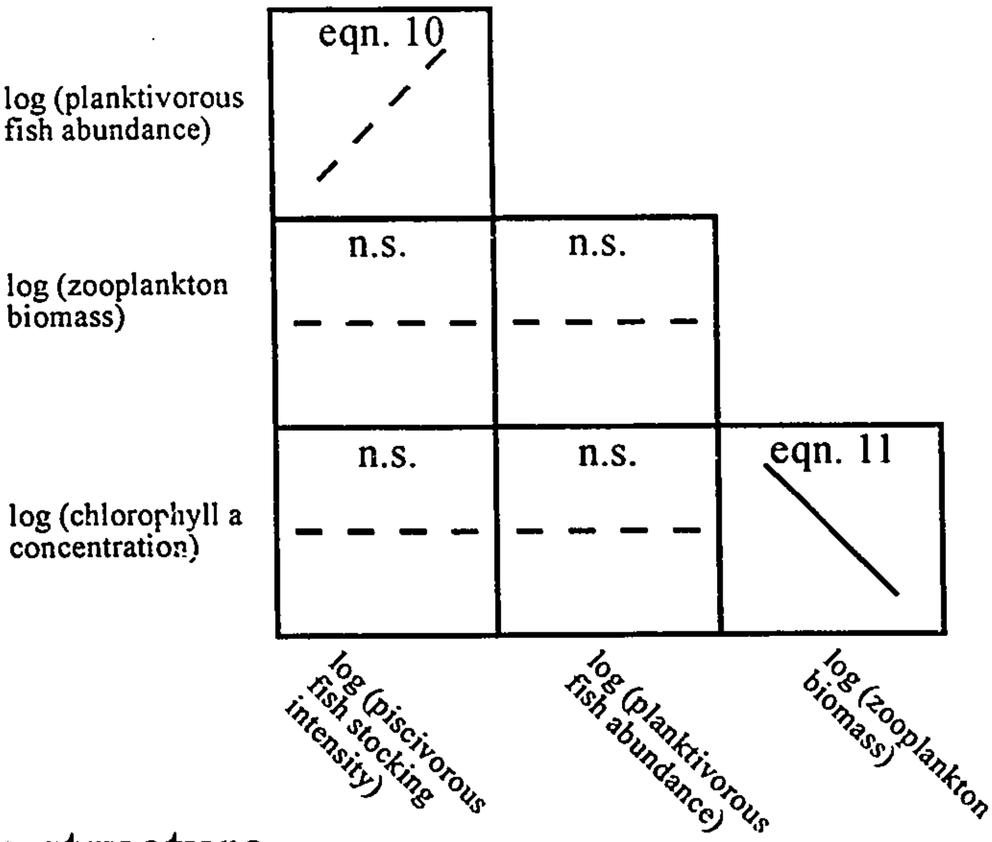

log Mean individual zooplankton dry mass (µg dry mass individual^{-1})
0.00
-0.25
-0.50
-0.75
-1.00
-1.25
A
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
log Total phosphorus (µg l^{-1})
B
-0.25
0.00
0.25
0.50
0.75
1.00
log Chlorophyll *a* (µg l^{-1})
● stocked lakes
○ non-stocked lakes

Figure 7. Schematic representation of the results for the cascading trophic interactions hypothesis for trophic level biomass and abundance, and size structure as they apply to a series of lakes differing in piscivorous fish stocking intensity, in each case adjusting for log total phosphorus as a linear covariate. Dashed horizontal lines represent non-significant relationships. Solid lines with non-zero slope indicate significant relationships ($P < 0.05$, equations listed in Table 3). Dashed lines with non-zero slope represent nearly significant relationships ($0.05 < P < 0.15$).

Biomass.



Size structure.

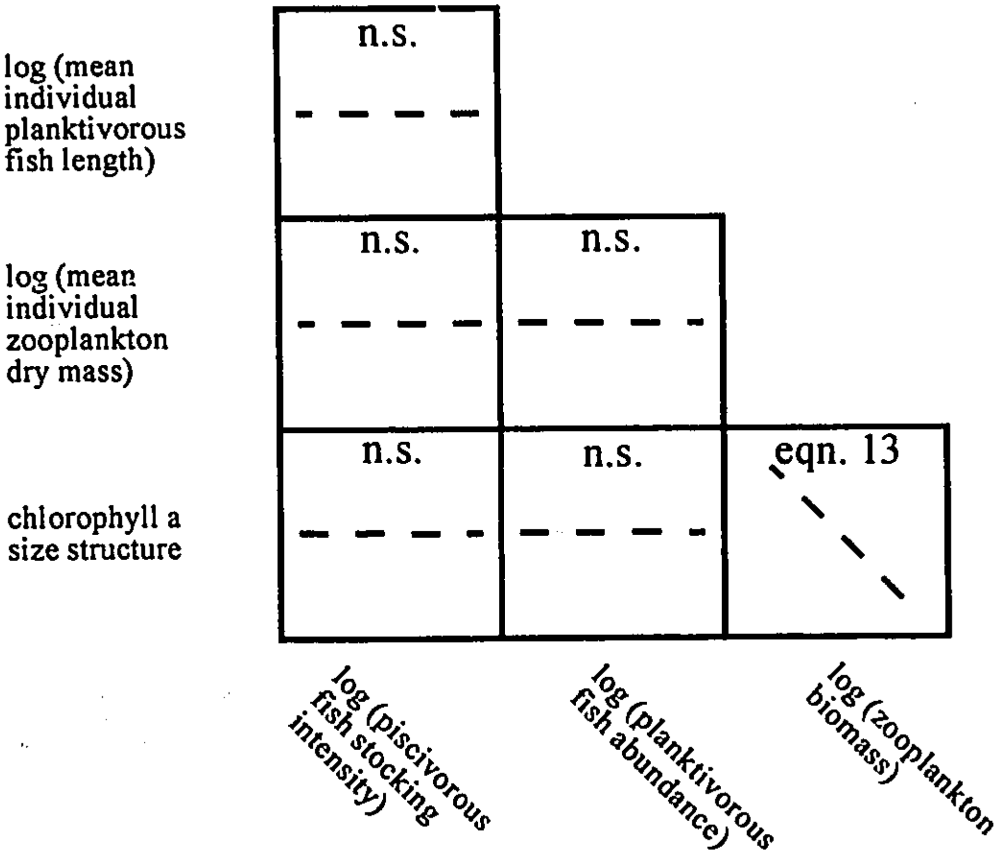


Figure 8. The relationships between: A. log planktivorous fish abundance ($r^2 = 0.01$, $n = 31$, $P = 0.146$ including non-stocked lakes, $r^2 = 0.21$, $n = 24$, $P = 0.029$ excluding non-stocked lakes); and B. log mean individual planktivorous fish length ($r^2 = 0.01$, $n = 31$, $P = 0.230$), in each case as functions of log piscivorous fish stocking intensity and adjusting for log total phosphorus as a linear covariate. Stocking intensity measured as the total number of fish stocked in 6 years prior to sampling Ha^{-1}. Filled circles represent lakes stocked with piscivorous sport fish, open circles represent non-stocked lakes.

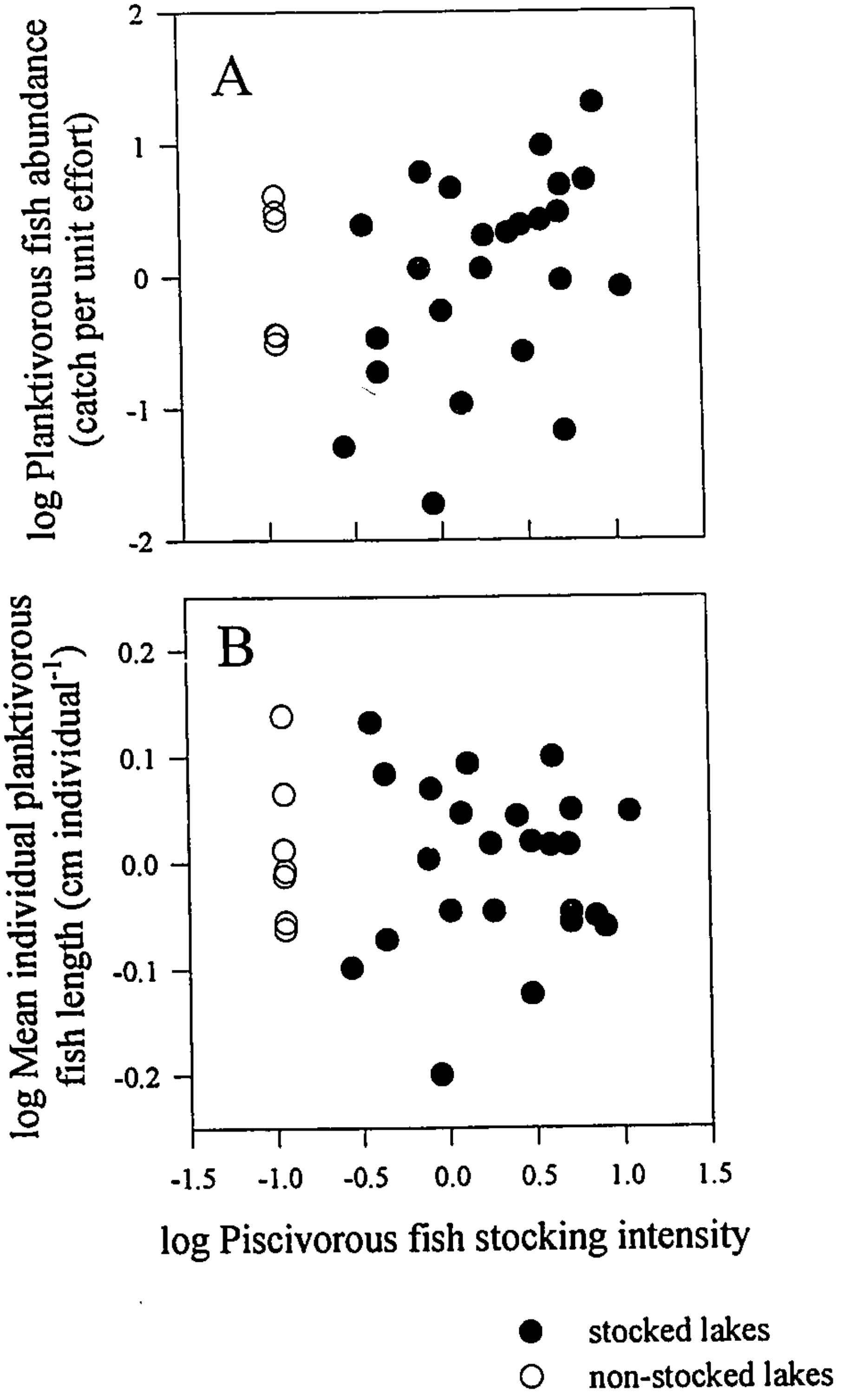

A
B
2
1
0
-1
-2
log Planktivorous fish abundance
(catch per unit effort)
0.2
0.1
0.0
-0.1
-0.2
log Mean individual planktivorous
fish length (cm individual^{-1})
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
log Piscivorous fish stocking intensity
● stocked lakes
○ non-stocked lakes

Figure 9. The relationships between: A. log zooplankton biomass ($r^2 < 0.01$, $n = 31$, $P = 0.97$); B. log mean individual zooplankton dry mass ($r^2 < 0.01$, $n = 31$, $P = 0.87$); and C. log chlorophyll *a* ($r^2 < 0.01$, $n = 31$, $P = 0.92$), in each case as functions of log piscivorous fish stocking intensity and adjusting for log total phosphorus as a linear covariate. Stocking intensity measured as the total number of fish stocked in 6 years prior to sampling Ha^{-1}. Filled circles represent lakes stocked with piscivorous sport fish, open circles represent non-stocked lakes.

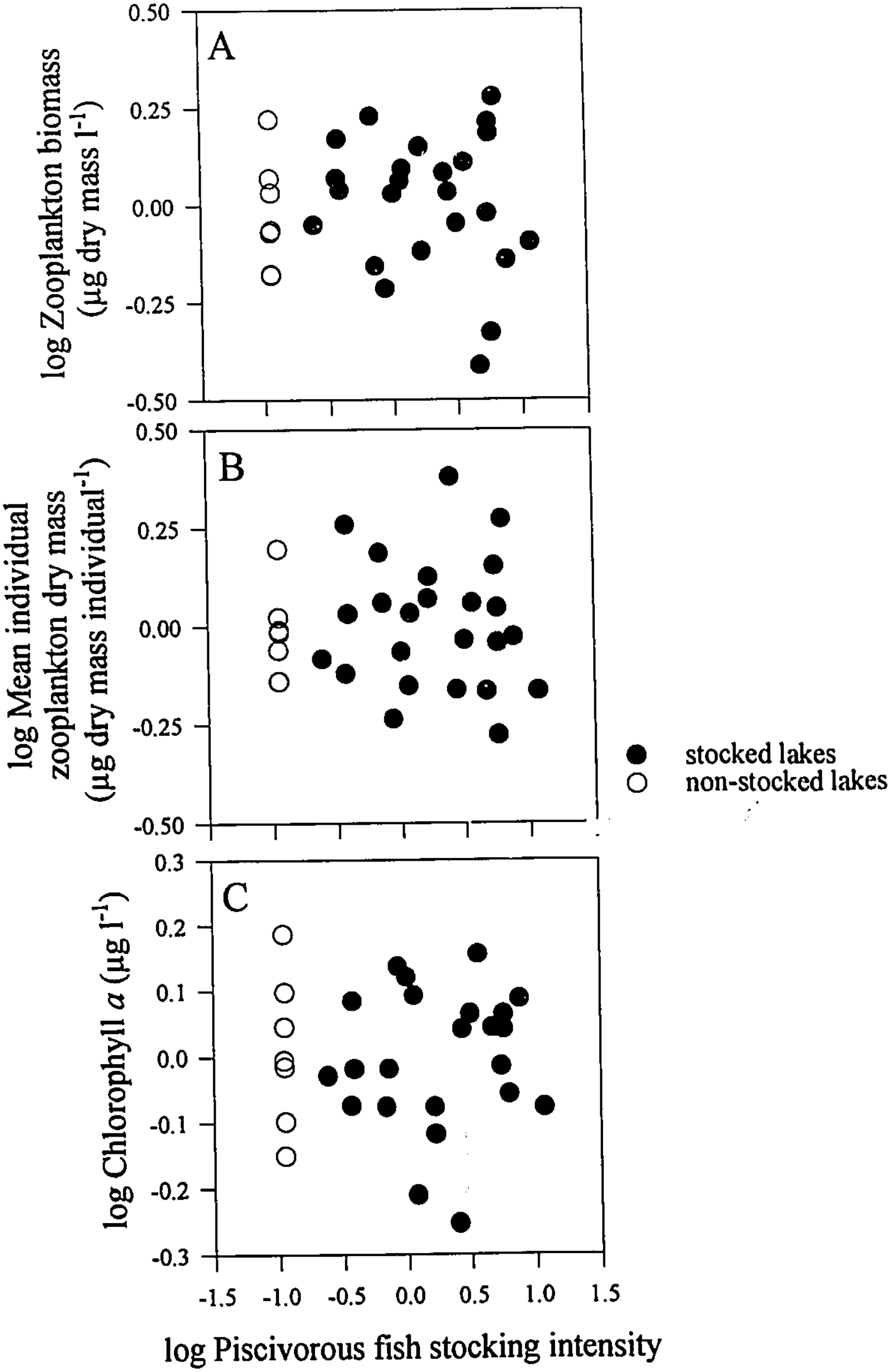

A
B
C
0.50
0.25
0.00
-0.25
-0.50
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
log Zooplankton biomass (μg dry mass l^{-1})
log Mean individual zooplankton dry mass (μg dry mass individual^{-1})
log Chlorophyll *a* (μg l^{-1})
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
log Piscivorous fish stocking intensity
● stocked lakes
○ non-stocked lakes

Figure 10. The relationship between: A. log chlorophyll *a* and log zooplankton biomass ($r^2 = 0.12$, $n = 31$, $P = 0.056$); and B. log chlorophyll *a* and log mean individual zooplankton dry mass ($r^2 = 0.23$, $n = 31$, $P = 0.054$), in each case adjusting for log total phosphorus as a linear covariate. Filled circles represent lakes stocked with piscivorous sport fish, open circles represent non-stocked lakes.

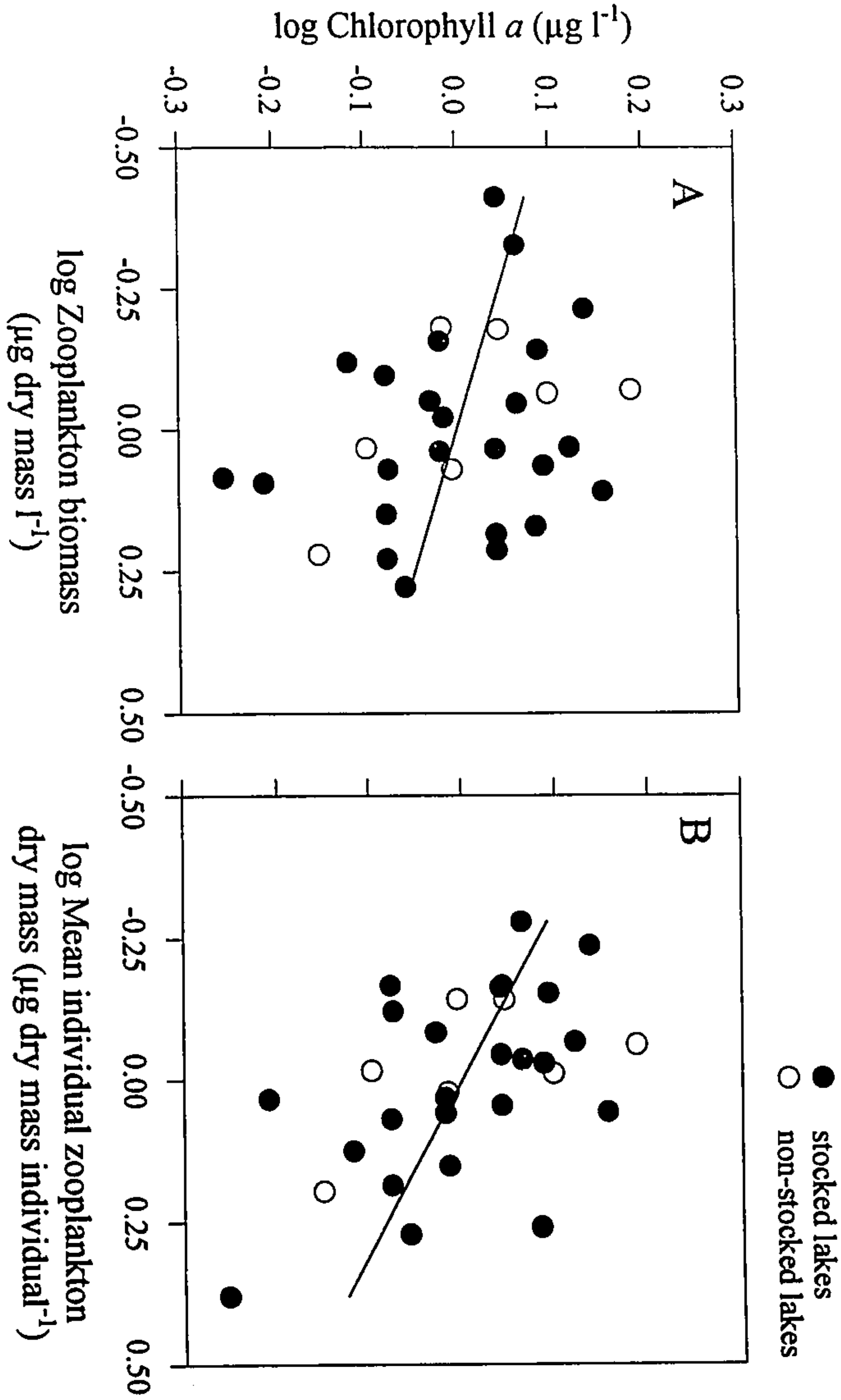

log Chlorophyll a (µg l-1)
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
A
-0.50
-0.25
0.00
0.25
0.50
log Zooplankton biomass (µg dry mass l-1)
B
-0.50
-0.25
0.00
0.25
0.50
log Mean individual zooplankton dry mass (µg dry mass individual-1)
● stocked lakes
○ non-stocked lakes

Figure 11. The relationship between log zooplankton abundance and log planktivorous fish abundance ($r^2 = 0.41$, $n = 31$, $P < 0.001$), adjusting for log total phosphorus as a linear covariate. Filled circles represent lakes stocked with piscivorous sport fish, open circles represent non-stocked lakes.

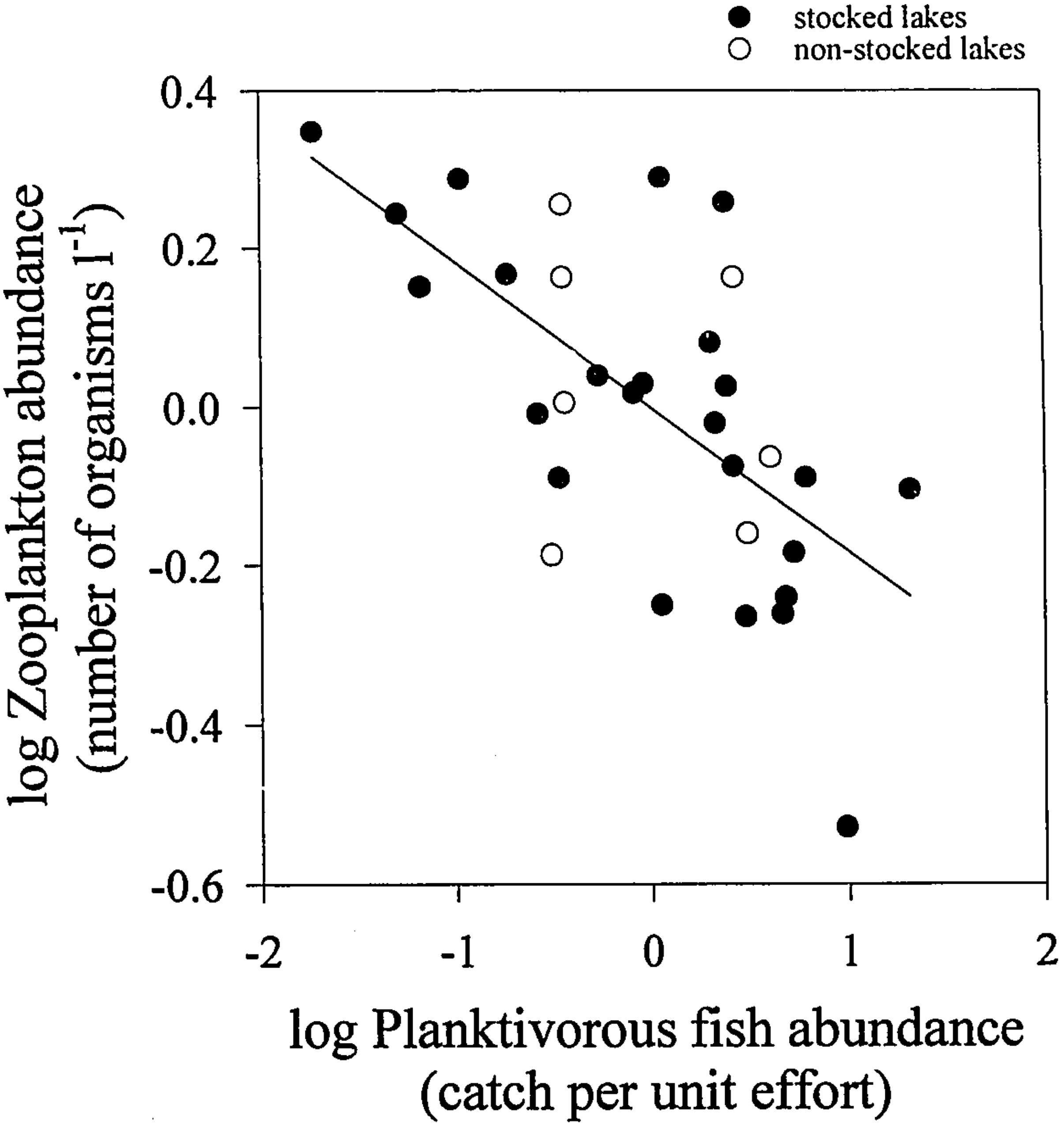
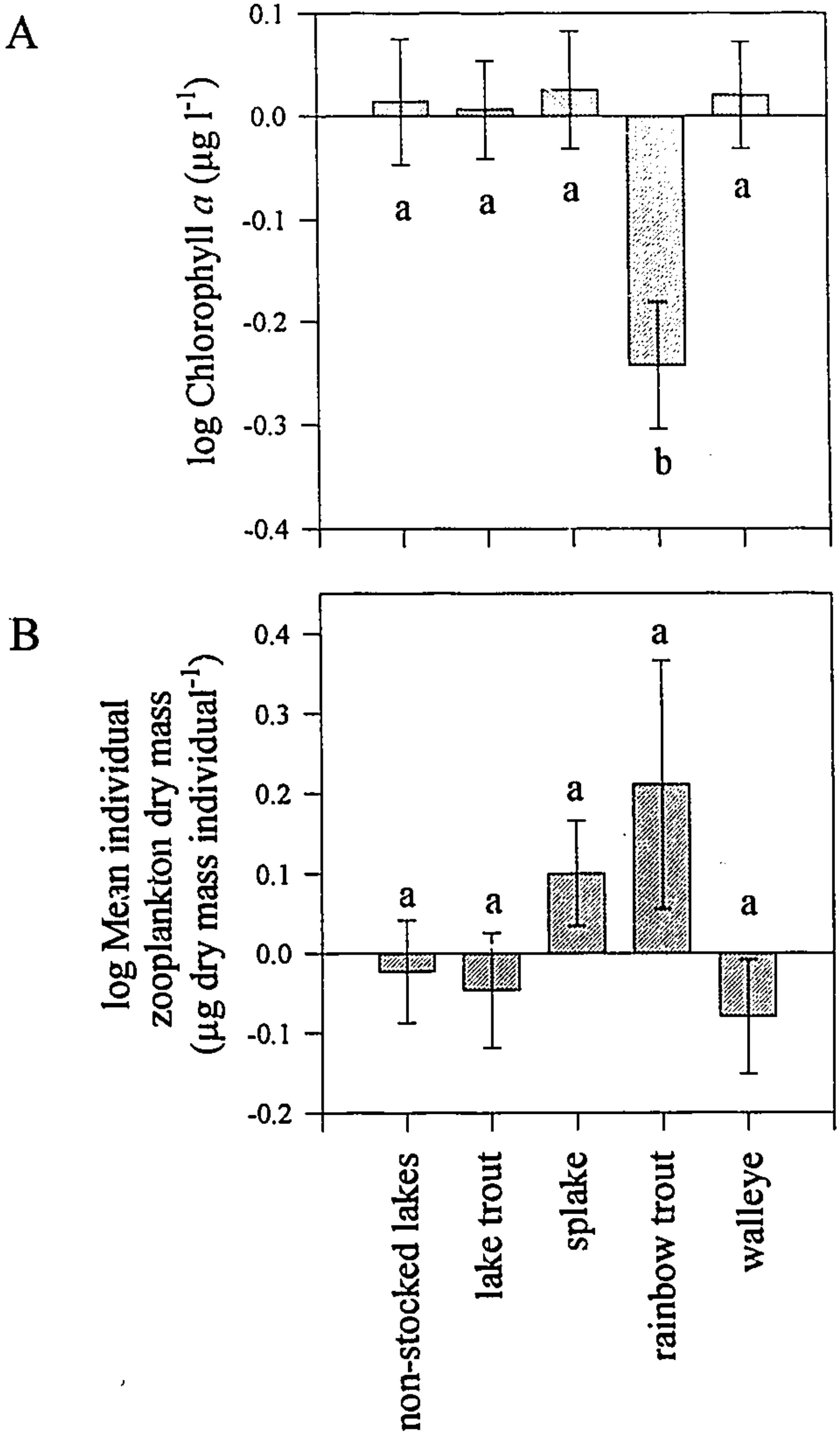

● stocked lakes
○ non-stocked lakes
0.4
0.2
0.0
-0.2
-0.4
-0.6
-2
-1
0
1
2
log Zooplankton abundance (number of organisms l^{-1})
log Planktivorous fish abundance (catch per unit effort)

Figure 12. The effect of piscivorous sport fish species stocked on: A. chlorophyll *a* concentration; and B. mean individual zooplankton dry mass, in each case adjusting for log total phosphorus as a linear covariate. The analysis of covariance showed there to be significant differences among groups in both cases. Bars with different letters (a or b) are significantly different in pairwise *a posteriori* comparisons (Tukey test, $P < 0.05$). Error bars represent ± 1 standard error.


A
log Chlorophyll a (µg l-1)
0.1
0.0
-0.1
-0.2
-0.3
-0.4
a
a
a
b
a
B
log Mean individual zooplankton dry mass (µg dry mass individual-1)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
a
a
a
a
a
non-stocked lakes
lake trout
splake
rainbow trout
walleye

Appendix 1. Location, surface area, and piscivorous fish species stocked in the 31 sample lakes.

Lake	Surface area (Ha)	Latitude	Longitude	Species stocked
Crow	442	44° 36'	76° 25	*Salvelinus namaycush*
Eagle	646	44° 41'	76° 42'	*Salvelinus namaycush*
Little Green	29	44° 58'	76° 53'	*Salvelinus namaycush*
Mazinaw	1590	44° 55'	77° 12'	*Salvelinus namaycush*
Palmerston	563	45° 01'	76° 51'	*Salvelinus namaycush*
Shabomeeka	268	44° 54'	77° 08'	*Salvelinus namaycush*
Silver	246	44° 36'	76° 30'	*Salvelinus namaycush*
Mair	49	45° 07'	76° 50'	*Oncorhynchus mykiss*
Mosque	138	45° 01'	76° 55'	*Oncorhynchus mykiss*
Cronk	35	44° 28'	76° 34'	F1 *S. namaycush* X *S. fontinalis*
Egg	10	45° 05'	76° 48'	F1 *S. namaycush* X *S. fontinalis*
Granite	24	45° 04'	76° 52'	F1 *S. namaycush* X *S. fontinalis*
Grindstone	173	45° 01'	76° 57'	F1 *S. namaycush* X *S. fontinalis*
Otter	571	44° 46'	76° 13'	F1 *S. namaycush* X *S. fontinalis*
Upper Rock	76	44° 30'	76° 24'	F1 *S. namaycush* X *S. fontinalis*
White	183	44° 36'	76° 37'	F1 *S. namaycush* X *S. fontinalis*
13 Island	106	44° 32'	76° 38'	*Stizostedion vitreum*
Flower Round	97	45° 10'	76° 41'	*Stizostedion vitreum*
Hambly	90	44° 28'	76° 21'	*Stizostedion vitreum*
Joe's	60	45° 08'	76° 38'	*Stizostedion vitreum*
Upper Park	56	45° 01'	76° 36'	*Stizostedion vitreum*
Sand (Bedford)	25	44° 34'	76° 35'	*Stizostedion vitreum*
Sand (Plevna)	179	44° 34'	77° 02'	*Stizostedion vitreum*
Black	45	44° 47'	76° 43'	*Stizostedion vitreum*
Buckshot	420	45° 00'	77° 04'	--
Otty	633	44° 51'	76° 13'	--
Patterson	152	45° 01'	76° 32'	--
Pike	349	44° 47'	76° 21'	--
Red Horse	103	45° 06'	76° 48'	--
Robertson	64	45° 04'	76° 39'	--
St. George	71	44° 44'	76° 41'	--

Appendix 2. Summary cf chemical and biological parameters obtained from the 31 lakes for the first sampling period (June 16 - July 10 199

Lake	Secchi depth (m)	pH	epilimnetic conductivity (µmhos cm^{2})	Total phosphorus (µg l^{-1})	Total chlorophyll a (µg l^{-1})	Chlorophyll *a* >35 µm (µg l^{-1})	Chlorophyll *a* 12-35 µm (µg l^{-1})	Chlorophyll *a* 2-12 µm (µg l^{-1})	Chlorophyll *a* <2 µm (µg l^{-1})
Crow	10.25	--	--	8.69	2.18	0.311	0.358	0.546	0.582
Eagle	5.75	--	125	7.26	1.48	0.336	0.415	0.408	0.386
Little Green	7.60	8.43	270	7.60	1.40	0.138	0.345	0.374	0.504
Mazinaw	5.50	--	70	4.86	1.41	0.105	0.155	0.395	0.607
Palmerston	7.75	8.25	185	6.87	1.15	0.169	0.298	0.308	0.281
Shabomecka	5.25	--	75	5.33	1.81	0.269	0.386	0.399	0.474
Silver	5.75	8.32	240	10.26	1.99	0.311	0.455	0.552	0.823
Mair	8.30	8.22	230	7.15	0.86	0.159	0.283	0.265	0.246
Mosque	7.25	7.84	185	7.77	1.08	0.300	0.146	0.250	0.430
Cronk	5.00	--	355	7.23	1.25	0.091	0.509	0.433	0.422
Egg	5.20	8.31	240	9.84	2.45	0.439	0.751	0.416	0.727
Granite	5.40	8.30	170	9.98	2.02	0.305	0.452	0.620	0.392
Grindstone	4.60	7.89	130	6.73	2.46	0.820	1.010	0.808	0.541
Otter	3.15	8.15	290	8.35	3.22	0.218	1.571	0.771	0.834
Upper Rock	4.25	--	175	8.75	3.10	0.392	1.263	0.643	0.647
White	6.20	--	230	9.03	1.27	0.404	0.255	0.391	0.385
13 Island	4.50	--	240	10.31	2.90	0.537	0.296	0.504	0.618
Flower Round	4.80	--	140	9.64	3.84	1.276	0.833	1.136	1.017
Hambly	3.75	--	310	11.60	3.10	0.583	0.415	1.233	1.009
Joe's	2.30	--	220	13.87	5.25	1.741	1.474	2.047	0.992
Upper Park	5.75	--	--	8.89	2.04	0.447	0.327	0.637	0.622
Sand (Bedford)	4.80	--	125	6.98	1.65	0.321	0.670	0.364	0.379
Sand (Plevna)	3.75	8.23	395	7.71	1.96	0.180	0.517	0.781	0.525
Black	5.80	8.29	260	10.26	1.45	0.228	0.251	0.653	0.472
Buckshot	5.80	7.30	140	6.90	2.85	0.462	0.504	0.769	0.868
Otty	4.75	--	220	12.44	2.37	0.299	0.421	0.598	1.175
Patterson	4.30	--	--	8.66	2.81	0.865	0.742	1.274	0.779
Pike	4.80	7.98	130	15.10	2.47	0.367	0.402	0.852	0.982
Red Horse	6.25	7.97	140	9.73	1.90	0.277	0.259	0.649	0.960
Robertson	7.90	--	270	6.23	1.62	0.366	0.354	0.519	0.426
St. George	7.50	--	175	11.40	2.76	0.536	0.399	0.745	0.828

Appendix 2. continued

Lake	Zooplankton biomass ($\mu g\ l^{-1}$)	Zooplankton density (number l^{-1})	Cladoceran biomass ($\mu g\ l^{-1}$)	Copepod biomass ($\mu g\ l^{-1}$)	Nauplii biomass ($\mu g\ l^{-1}$)	Rotifer biomass ($\mu g\ l^{-1}$)	Mean individual zooplankton dry mass (μg individual^{-1})	Mean individual cladoceran dry mass (μg individual^{-1})	Mean individual copepod dry mass (μg individual^{-1})
Crow	89.48	270.60	15.82	99.63	12.89	12.29	0.174	0.748	1.559
Eagle	135.65	218.71	58.92	54.99	9.80	11.94	0.193	1.612	1.406
Little Green	141.54	83.48	63.32	65.30	5.12	4.54	0.259	9.657	3.694
Mazinaw	99.10	146.83	21.61	61.45	11.40	4.64	0.224	0.541	2.348
Palmerston	74.13	78.10	33.01	30.16	5.45	3.02	0.279	3.511	1.303
Shabomeeka	107.07	239.13	31.00	50.21	14.43	11.43	0.154	1.309	1.494
Silver	238.89	139.91	133.65	92.73	8.93	3.58	0.459	3.462	1.838
Mair	103.97	87.33	9.66	114.50	9.02	3.08	0.457	5.531	3.805
Mosque	223.67	142.05	166.97	49.70	15.39	5.09	0.262	5.134	3.552
Cronk	169.53	208.95	49.13	101.77	9.07	9.56	0.243	3.538	1.332
Egg	119.26	124.50	72.27	26.10	22.55	3.59	0.244	2.970	2.213
Granite	262.66	318.65	110.37	167.53	19.81	7.67	0.376	1.196	1.510
Grindstone	113.93	105.37	74.50	24.88	5.28	5.99	0.246	2.258	2.400
Otter	161.37	126.05	133.36	31.27	10.09	4.06	0.413	2.406	1.221
Upper Rock	150.98	162.51	57.97	80.05	4.93	8.03	0.177	1.913	1.789
White	149.11	106.81	68.69	68.57	7.12	4.72	0.367	3.214	2.020
13 Island	195.82	211.00	143.82	31.20	8.24	12.56	0.153	3.862	1.683
Flower Round	81.70	198.67	23.51	31.20	20.54	6.45	0.186	1.394	1.325
Hambly	33.40	113.88	7.36	15.64	3.28	7.41	0.114	0.300	1.538
Joe's	63.54	512.77	5.62	16.93	14.22	26.77	0.076	0.252	1.119
Upper Park	367.50	121.65	341.21	14.93	5.78	5.59	0.167	2.142	1.151
Sand (Bedford)	151.28	57.97	135.89	8.55	3.97	2.87	0.240	7.840	1.817
Sand (Plevna)	97.25	98.05	5.37	71.94	7.32	5.16	0.253	3.834	2.845
Black	205.99	520.08	49.79	102.63	19.14	34.43	0.147	1.937	1.552
Buckshot	70.94	49.86	13.09	33.81	6.96	1.62	0.295	0.382	2.727
Otty	140.56	325.44	84.31	43.19	9.63	13.85	0.204	0.658	1.092
Patterson	65.12	93.84	46.57	7.27	6.82	4.46	0.159	1.801	1.070
Pike	102.93	477.32	1.50	57.97	9.29	32.45	0.272	4.262	2.544
Red Horse	63.37	72.07	16.90	60.97	7.87	3.76	0.298	15.016	3.592
Robertson	143.20	49.87	133.64	3.98	3.42	2.16	0.188	3.211	0.636
St. George	115.24	272.62	55.29	99.54	10.55	16.19	0.159	2.793	2.281

Appendix 2. continued

Lake	Mean individual nauplii dry mass (µg individual^{-1})	Mean individual rotifer dry mass (µg individual^{-1})	Piscivorous fish stocking intensity (no.stocked over 6 years prior to sampling Ha^{-1})
Crow	0.211	0.076	28
Eagle	0.258	0.085	46
Little Green	0.347	0.079	328
Mazinaw	0.262	0.073	106
Palmerston	0.353	0.076	85
Shabomeeka	0.242	0.076	134
Silver	0.201	0.087	80
Mair	0.280	0.097	318
Mosque	0.218	0.087	150
Cronk	0.192	0.089	195
Egg	0.292	0.083	936
Granite	0.254	0.059	743
Grindstone	0.324	0.089	124
Otter	0.217	0.085	43
Upper Rock	0.203	0.076	446
White	0.281	0.095	204
13 Island	0.210	0.082	749
Flower Round	0.192	0.086	405
Hambly	0.280	0.078	625
Joe's	0.282	0.060	751
Upper Park	0.213	0.074	760
Sand (Bedford)	0.197	0.092	1500
Sand (Plevna)	0.347	0.088	723
Black	0.244	0.088	46
Buckshot	0.265	0.092	0
Otty	0.179	0.080	0
Patterson	0.193	0.085	0
Pike	0.280	--	0
Red Horse	0.247	0.104	0
Robertson	0.225	0.077	0
St. George	0.207	0.082	0

Appendix 3. Summary of chemical and biological parameters obtained from the 31 lakes for the second sampling period (August 11 - Septe

Lake	Secchi depth (m)	pH	epilimnetic conductivity (µmhos cm^2)	Total phosphorus (µg l^{-1})	Total chlorophyll a (µg l^{-1})	Chlorophyll *a* >35 µm (µg l^{-1})	Chlorophyll *a* 12-35 µm (µg l^{-1})	Chlorophyll *a* 2-12 µm (µg l^{-1})	Chlorophyll *a* <2 µm (µg l^{-1})
Crow	5.60	8.31	145	6.93	1.95	0.136	0.202	0.441	0.705
Eagle	5.10	8.51	180	7.74	2.91	0.228	0.396	0.500	0.646
Little Green	6.15	7.49	375	4.66	1.48	0.140	0.338	0.496	0.329
Mazinaw	6.30	7.49	210	4.21	1.81	0.249	0.287	0.250	0.703
Palmerston	8.40	8.42	170	4.69	1.26	0.091	0.169	0.255	0.388
Shabomeeka	5.90	7.74	75	5.67	2.00	0.220	0.245	0.374	0.748
Silver	3.75	8.63	240	10.26	2.77	0.177	0.800	0.812	0.971
Mair	8.75	8.33	210	5.64	1.07	0.080	0.296	0.277	0.294
Mosque	7.10	7.99	105	6.67	1.39	0.143	0.133	0.338	0.718
Cronk	5.90	8.37	400	6.25	1.82	0.286	0.163	0.185	0.399
Egg	6.20	8.25	220	6.53	3.11	0.791	0.315	1.018	0.701
Granite	6.65	8.39	160	6.53	1.27	0.118	0.448	0.373	0.348
Grindstone	4.75	8.01	85	5.41	1.89	0.103	0.183	0.699	0.562
Otter	3.35	--	260	10.62	4.48	0.380	2.027	1.415	0.795
Upper Rock	5.50	8.51	280	6.59	2.82	0.193	0.428	0.326	0.692
White	3.80	8.38	230	4.91	1.76	0.010	0.426	0.581	0.360
13 Island	5.00	8.41	345	11.40	4.19	0.982	0.468	0.674	0.897
Flower Round	4.50	8.16	150	11.21	5.82	0.911	0.623	1.154	2.056
Hambly	4.50	8.44	335	10.29	3.42	0.805	0.377	0.579	0.994
Joe's	3.00	7.91	190	14.71	4.57	0.812	0.582	1.356	1.349
Upper Park	6.30	8.29	170	8.61	2.24	0.621	0.243	0.430	0.672
Sand (Bedford)	7.30	7.99	110	7.60	1.88	0.302	0.298	0.368	0.783
Sand (Plevna)	5.50	8.42	225	5.64	1.47	0.162	0.351	0.481	0.416
Black	5.75	8.50	270	6.39	1.53	0.150	0.514	0.610	0.525
Buckshot	5.55	7.68	80	5.58	2.06	0.863	0.445	0.224	0.580
Otty	4.40	--	210	13.56	3.52	0.539	0.946	1.330	1.016
Patterson	6.65	8.28	305	7.71	2.79	0.677	0.393	0.588	0.694
Pike	2.70	--	150	14.12	10.69	2.188	4.023	2.458	1.839
Red Horse	7.30	8.09	115	8.10	2.90	1.008	0.302	0.961	0.886
Robertson	9.30	8.38	180	6.25	1.76	0.455	0.156	0.275	0.530
St. George	6.00	8.36	195	7.07	1.35	0.215	0.191	0.168	0.438

Appendix 3. continued

Lake	Zooplankton biomass (μg l^{-1})	Zooplankton density (number l^{-1})	Cladoceran biomass (μg l^{-1})	Copepod biomass (μg l^{-1})	Nauplii biomass (μg l^{-1})	Rotifer biomass (μg l^{-1})	Mean individual zooplankton dry mass (μg individual^{-1})	Mean individual cladoceran dry mass (μg individual^{-1})	Mean individual copepod dry mass (μg individual^{-1})
Crow	56.11	96.75	14.79	33.91	3.69	3.71	0.15	0.724	1.224
Eagle	115.07	119.43	54.73	48.03	8.20	4.11	0.25	2.849	1.231
Little Green	74.66	102.10	12.49	52.82	5.75	3.60	0.18	1.425	1.130
Mazinaw	25.70	53.54	9.21	10.68	3.71	2.10	0.15	1.324	2.012
Palmerston	30.44	52.73	2.68	21.84	4.61	1.32	0.22	0.501	1.212
Shabomecka	71.99	103.86	20.71	43.17	4.57	3.54	0.22	1.526	1.436
Silver	140.26	110.95	76.07	53.23	8.98	1.98	0.36	3.019	1.355
Mair	119.63	50.96	44.79	71.36	3.20	0.28	1.00	1.467	2.472
Mosque	110.85	61.92	85.22	18.44	5.69	1.50	0.24	4.384	1.253
Cronk	120.09	117.78	45.20	63.33	8.71	2.85	0.28	3.139	1.111
Egg	56.57	68.90	31.92	15.67	7.23	1.74	0.20	5.440	0.668
Granite	267.48	124.46	211.49	48.30	6.19	1.50	0.53	2.629	1.388
Grindstone	113.81	106.10	45.95	56.25	8.13	3.48	0.21	6.002	2.221
Otter	165.50	84.09	109.09	49.92	5.60	0.89	0.45	3.421	1.327
Upper Rock	81.68	103.80	42.10	32.24	3.56	3.79	0.17	2.249	1.249
White	55.76	48.32	21.35	28.55	5.53	0.32	0.39	1.811	1.105
13 Island	116.93	246.21	31.50	63.58	13.60	8.25	0.18	0.949	0.592
Flower Round	74.30	150.39	22.16	40.84	5.69	5.61	0.15	0.530	1.261
Hambly	56.01	379.27	6.88	23.84	7.98	17.31	0.09	0.274	0.388
Joe's	128.54	543.82	8.37	87.92	13.11	19.15	0.11	0.214	0.572
Upper Park	390.08	76.04	358.19	25.04	4.83	2.01	0.41	10.382	1.058
Sand (Bedford)	90.90	135.72	62.00	15.14	5.77	7.99	0.14	11.073	0.466
Sand (Plevna)	81.24	35.42	45.09	33.07	2.56	0.52	0.48	4.082	2.021
Black	79.52	184.56	10.29	52.07	8.01	9.16	0.16	1.920	0.968
Buckshot	80.84	95.96	44.69	26.30	4.64	5.21	0.16	4.341	1.414
Otty	120.63	350.50	54.53	42.56	10.40	13.15	0.14	1.000	0.429
Patterson	208.35	142.94	143.81	49.64	11.49	3.40	0.22	3.380	2.064
Pike	144.96	242.12	86.78	39.70	10.99	7.50	0.14	3.405	0.816
Red Horse	66.63	141.16	12.06	42.66	7.81	4.09	0.19	0.301	1.246
Robertson	95.33	47.59	81.62	8.26	4.06	1.39	0.23	4.418	0.638
St. George	253.77	93.22	205.66	40.44	5.89	1.77	0.45	3.813	1.450

Appendix 3. continued

Lake	Mean individual nauplii dry mass (μg individual^{-1})	Mean individual rotifer dry mass (μg individual^{-1})	Piscivorous fish stocking intensity (no.stocked over 6 years prior to sampling Ha^{-1})
Crow	0.196	0.065	28
Eagle	0.193	0.081	46
Little Green	0.215	0.066	328
Mazinaw	0.238	0.064	106
Palmerston	0.232	0.065	85
Shabomeeka	0.165	0.072	134
Silver	0.191	0.069	80
Mair	0.220	0.089	318
Mosque	0.178	0.068	150
Cronk	0.213	0.069	195
Egg	0.284	0.059	936
Granite	0.130	0.069	743
Grindstone	0.205	0.066	124
Otter	0.150	0.066	43
Upper Rock	0.195	0.060	446
White	0.193	0.070	204
13 Island	0.148	0.082	749
Flower Round	0.143	0.070	405
Hambly	0.130	0.063	625
Joe's	0.128	0.058	751
Upper Park	0.177	0.077	760
Sand (Bedford)	0.145	0.093	1500
Sand (Plevna)	0.195	0.064	723
Black	0.189	0.081	46
Buckshot	0.200	0.083	0
Otty	0.167	0.065	0
Patterson	0.174	0.064	0
Pike	0.124	0.060	0
Red Horse	0.171	0.077	0
Robertson	0.186	0.072	0
St. George	0.148	0.077	0

Appendix 4. Summary of chemical and biological parameters obtained from the 31 lakes for the third sampling period (June 15 - August 4

Lake	Secchi depth (m)	pH	epilimnetic conductivity (µmhos cm^2)	Total phosphorus (µg l^{-1})	Total chlorophyll a (µg l^{-1})	Chlorophyll *a* >35 µm (µg l^{-1})	Chlorophyll *a* 12-35 µm (µg l^{-1})	Chlorophyll *a* 2-12 µm (µg l^{-1})	Chlorophyll *a* <2 µm (µg l^{-1})
Crow	6.25	8.07	130	9.29	2.43	0.273	0.526	0.648	0.657
Eagle	5.50	8.33	125	10.30	2.66	0.176	0.938	0.718	0.617
Little Green	6.25	8.48	255	3.79	2.03	0.182	0.580	0.593	0.536
Mazinaw	5.75	--	80	3.95	1.95	0.353	0.788	0.673	1.126
Palmerston	7.00	8.51	260	4.03	1.86	0.214	0.703	0.402	0.776
Shabomeeka	5.75	7.90	85	6.20	2.28	0.436	0.906	0.584	0.633
Silver	5.50	8.61	270	10.46	2.60	0.355	0.227	0.583	0.916
Mair	6.00	8.24	290	5.03	0.89	0.089	0.249	0.219	0.298
Mosque	7.00	7.89	115	7.80	1.43	0.212	0.303	0.393	0.667
Cronk	5.75	8.43	220	8.73	2.32	0.089	1.304	0.468	0.434
Egg	3.25	8.50	275	9.09	3.16	0.389	0.739	1.303	0.822
Granite	4.00	8.75	170	11.14	4.26	0.241	2.510	0.907	0.547
Grindstone	4.25	8.06	85	6.32	2.63	0.229	1.093	0.893	0.714
Otter	3.75	--	255	11.30	2.74	0.583	0.673	0.759	0.689
Upper Rock	4.00	8.52	175	9.01	3.94	0.491	1.196	0.796	0.900
White	4.75	8.23	390	6.04	1.22	0.062	0.446	0.284	0.385
13 Island	4.75	8.48	230	18.94	5.28	2.249	1.186	1.676	0.813
Flower Round	5.25	--	145	10.42	1.73	0.212	0.261	0.313	0.636
Hambly	4.50	8.45	345	11.14	3.70	0.610	0.609	0.745	1.325
Joe's	2.50	7.90	200	23.72	6.60	1.363	1.161	2.169	1.866
Upper Park	4.25	8.42	215	12.35	6.08	1.649	1.065	2.410	1.278
Sand (Bedford)	5.25	8.07	130	10.30	2.32	0.343	0.303	0.672	1.002
Sand (Plevna)	5.50	8.43	175	4.55	1.44	0.172	0.455	0.741	0.536
Black	4.75	8.47	280	6.96	2.80	0.152	1.039	0.869	0.730
Buckshot	4.50	7.53	115	4.67	2.61	0.939	0.504	0.513	0.737
Otty	3.00	--	235	17.33	3.81	0.827	0.520	1.338	1.040
Patterson	5.25	8.46	180	9.97	2.59	0.203	0.339	0.790	0.978
Pike	3.75	--	215	16.36	5.52	2.063	1.304	0.816	1.539
Red Horse	5.75	8.12	155	8.93	2.57	0.406	1.031	0.417	0.674
Robertson	7.00	8.11	265	6.00	1.83	0.156	0.224	0.545	0.706
St. George	5.00	8.46	195	9.89	1.68	0.174	0.196	0.343	0.574

Appendix 4. continued

Lake	Zooplankton biomass (μg l^{-1})	Zooplankton density (number l^{-1})	Cladoceran biomass (μg l^{-1})	Copepod biomass (μg l^{-1})	Nauplii biomass (μg l^{-1})	Rotifer biomass (μg l^{-1})	Mean individual zooplankton dry mass (μg individual^{-1})	Mean individual cladoceran dry mass (μg individual^{-1})	Mean individual copepod dry mass (μg individual^{-1})
Crow	233.32	281.90	86.66	121.34	16.10	9.21	0.24	2.826	1.236
Eagle	140.84	147.96	71.78	57.81	7.83	3.42	0.28	1.427	1.135
Little Green	113.22	101.67	57.61	46.85	4.79	3.97	0.17	2.839	1.487
Mazinaw	69.08	131.27	19.71	34.24	11.49	3.64	0.19	0.786	1.879
Palmerston	140.39	49.12	100.70	34.71	4.24	0.74	0.61	4.094	2.220
Shabomeeka	216.24	194.17	84.03	112.95	12.90	6.35	0.27	2.865	2.450
Silver	312.38	360.22	206.27	75.15	17.09	13.87	0.17	2.890	1.411
Mair	159.82	74.72	74.34	77.37	7.13	0.98	0.59	2.108	3.075
Mosque	112.50	71.94	62.50	40.25	8.09	1.66	0.27	4.344	2.964
Cronk	199.29	179.96	80.20	105.02	10.53	3.54	0.32	3.961	1.173
Egg	94.23	123.35	50.14	30.65	9.40	4.04	0.19	1.142	0.868
Granite	177.77	130.29	143.14	23.81	8.12	2.69	0.32	2.723	1.100
Grindstone	111.60	111.96	39.79	59.34	8.86	3.60	0.22	4.103	3.044
Otter	253.66	297.62	124.92	107.83	11.74	9.17	0.26	1.367	1.315
Upper Rock	278.09	130.71	99.95	168.39	7.55	2.20	0.58	5.162	2.305
White	65.88	54.52	22.50	38.33	3.83	1.22	0.28	2.653	1.352
13 Island	542.25	213.52	318.62	208.18	7.51	7.95	0.26	11.928	3.847
Flower Round	261.52	180.62	193.61	52.76	9.71	5.44	0.22	3.329	0.963
Hambly	72.29	59.03	30.70	34.50	5.76	1.34	0.21	3.540	1.025
Joe's	49.37	686.16	3.71	4.75	5.52	35.39	0.06	0.196	0.588
Upper Park	50.88	240.47	23.70	9.34	4.60	13.24	0.09	0.245	0.881
Sand (Bedford)	61.64	188.89	18.43	27.10	5.40	10.71	0.11	1.391	0.979
Sand (Plevna)	120.62	37.84	98.90	18.54	2.37	0.81	0.47	3.675	1.349
Black	151.26	121.75	83.42	56.65	6.92	4.27	0.24	5.313	1.644
Buckshot	114.11	72.73	71.48	29.75	11.75	1.13	0.30	5.909	2.218
Otty	235.49	602.65	93.28	106.86	10.47	24.88	0.14	0.683	1.114
Patterson	38.41	121.05	12.08	14.59	6.97	4.76	0.11	2.225	1.806
Pike	146.77	455.89	4.42	104.50	16.74	21.11	0.10	1.216	1.710
Red Horse	123.01	132.76	67.45	33.61	19.62	2.32	0.20	10.765	2.391
Robertson	139.62	62.57	125.56	7.44	4.57	2.04	0.16	10.000	0.593
St. George	298.43	252.47	196.64	81.77	9.46	10.55	0.50	3.791	1.840

Appendix 4. continued

Lake	Mean individual nauplii dry mass (µg individual^{-1})	Mean individual rotifer dry mass (µg individual^{-1})	Planktivorous fish abundance (catch per unit effort)	Mean individual planktivorous fish length (cm indvidual^{-1})	Piscivorous fish stocking intensity (no.stocked over 6 years prior to sampling Ha^{-1})
Crow	0.188	0.074	4	5.50	34
Eagle	0.165	0.070	28	5.91	54
Little Green	0.192	0.068	438	4.74	379
Mazinaw	0.205	0.068	1	4.00	112
Palmerston	0.225	0.072	333	7.45	102
Shabomeeka	0.180	0.071	7	8.21	166
Silver	0.225	0.063	96	7.04	96
Mair	0.231	0.075	129	7.18	318
Mosque	0.219	0.067	341	7.54	150
Cronk	0.197	0.061	157	6.17	229
Egg	0.206	0.073	1598	5.99	986
Granite	0.161	0.066	457	6.25	870
Grindstone	0.216	0.068	36	5.99	130
Otter	0.197	0.069	16	8.53	54
Upper Rock	0.198	0.068	207	7.14	485
White	0.182	0.064	74	6.88	221
13 Island	0.185	0.065	529	6.66	624
Flower Round	0.178	0.064	22	7.30	374
Hambly	0.172	0.071	827	8.83	500
Joe's	0.207	0.055	8	8.50	626
Upper Park	0.168	0.070	79	6.25	626
Sand (Bedford)	0.211	0.072	68	7.78	1375
Sand (Plevna)	0.191	0.075	174	6.68	625
Black	0.161	0.079	172	9.09	46
Buckshot	0.221	0.088	21	8.86	0
Otty	0.185	0.064	37	6.47	0
Patterson	0.194	0.059	254	6.03	0
Pike	0.228	0.060	276	7.19	0
Red Horse	0.207	0.064	318	6.69	0
Robertson	0.171	0.068	20	6.80	0
St. George	0.200	0.067	28	8.07	0

Appendix 5. Summary of total fish species and numbers of individuals caught during third sampling period (June 16 - July 10 1994)

Lake	unidentified sunfish	*Lepomis gibbosus* pumpkin seed	*Lepomis macrochirus* bluegill	*Ambolites rupestris* rock bass	*Micropterus dolomieui* smallmouth bass	*Micropterus salmoides* largemouth bass	*Pomoxis nigromaculatus* black crappie	*Catostomus commersoni* white sucker	*Ictalurus nebulosus* brown bullhead
Crow	5	10	15		3	2			
Eagle	88	47	110	3	4	7			
Little Green		26		8	2				
Mazinaw					10	2			
Palmerston		3			8				
Shabomeeka		38			4	3		1	
Silver	262			10	1	8			
Mair		122						1	
Mosque		70							1
Cronk	334	9	45				8		
Egg		247		19					
Granite		100							
Grindstone		27			30	2			
Otter	68			1					1
Upper Rock	167	60	20	6	4		2		
White	133	121			1				
13 Island	24	146	35	21	5		15		
Flower Round	19	69	16	5	1				
Hambly	163	47	74	6	11		1		
Joe's		15			1	1			
Upper Park		50		1					
Sand (Bedford)		84			10				1
Sand (Plevna)		26			15	1			
Black		115	59	3	4	9			
Buckshot		9		1	26				
Otty	71			17	2	3			
Patterson	15	43		7					3
Pike	856			3					3
Red Horse		214			26	11			
Robertson	59	36	1		6				1
St George	111			3		1			

Appendix 5. continued

Lake	*Perca flavescens* yellow perch	*Stizostedion vitreum* walleye	*Etheostoma exile* iowa darter	*Percina caprodes* logperch	*Esox lucius* northern pike	*Umbra limi* central mudminnow	*Fundulus diaphanus* banded killifish	*Labidesthes sicculus* brook silverside	*Phoxinus eos* northern redbelly dace	*Couesius plumbeus* lake chub
Crow				1			1			
Eagle	9				2					
Little Green	15									
Mazinaw	159			1						
Palmerston	272									
Shabomeeka	45			1						
Silver	5			1						
Mair	2170								11	
Mosque	134						6			
Cronk	29				2		18			
Egg	119									
Granite	419									
Grindstone	4									
Otter	2			6						
Upper Rock	97		1	13			5			
White	66			16			22			
13 Island	103			15			44	3		
Flower Round	19			2						
Hambly	792			11				8		
Joe's				7						1
Upper Park	10	4			1					
Sand (Bedford)	70									
Sand (Plevna)	8									
Black	65			3	1	1				
Buckshot	1									
Otty	24									
Patterson	64				2		66			
Pike	159			49						
Red Horse	221				1					
Robertson	11						2			
St George	31			7						

Appendix 5. continued

Lake	*Hybognathus nuchalis* silvery minnow	*Notemigonus crysoleucas* golden shiner	*Notropis atherinoides* emerald shiner	*Notropis cornutus* common shiner	*Notropis heterodon* blackchin shiner	*Notropis heterolepis* blacknose shiner	*Pimephales notatus* bluntnose minnow	*Pimephales promelas* fathead minnow	*Semotilus atromaculatus* creek chub	*Semotilus corporalis* fallfish
Crow							2			
Eagle		7					16			
Little Green			411				20			
Mazinaw										
Palmerston	1						70			
Shabomecka							1			
Silver						91				
Mair		34					47	10		
Mosque	1	99					136	21		3
Cronk		90					31			
Egg		220	895	8	44		115	197		
Granite		5					424	15	5	
Grindstone							32			
Otter		4	2				3			
Upper Rock		12					126			
White							9			
13 Island		60					350			
Flower Round			1							
Hambly		19								
Joe's										
Upper Park		36	6				32			
Sand (Bedford)		4					26			
Sand (Plevna)		9					157			
Black		114			5		2			
Buckshot	14						6			
Otty						35	2			
Patterson		66			45		68			
Pike			11			65				
Red Horse		3					166			
Robertson		2					10			
St George			13				6			

Appendix 6. Summary of fish species and numbers used for the index of planktivorous fish abundance and size structure.

Lake	*Perca flavescens* yellow perch	*Etheostoma exile* iowa darter	*Percina caprodes* logperch	*Umbra limi* central mudminnow	*Fundulus diaphanus* banded killifish	*Labidesthes sicculus* brook silverside	*Phoxinus eos* northern redbelly dace	*Couesius plumbeus* lake chub	*Hybognathus nuchalis* silvery minnow
Crow			1		2				
Eagle	5								
Little Green	7								
Mazinaw			1						
Palmerston	262								1
Shabomeeka	5		1						
Silver	4		1						
Mair	27						11		
Mosque	75				6				1
Cronk	18				18				
Egg	119								
Granite	8								
Grindstone	4								
Otter	1		6						
Upper Rock	50	1	13		5				
White	27		16		22				
13 Island	57		15		44	3			
Flower Round	19		2						
Hambly	789		11			8			
Joe's			7					1	
Upper Park	5								
Sand (Bedford)	38								
Sand (Plevna)	8								
Black	47		3	1					
Buckshot	1								14
Otty									
Patterson	9				66				
Pike	151		49						
Red Horse	149								
Robertson	6				2				
St George	2		7						

Appendix 6. continued

Lake	*Notemigonus crysoleucas* golden shiner	*Notropis atherinoides* emerald shiner	*Notropis cornutus* common shiner	*Notropis heterodon* blackchin shiner	*Notropis heterolepis* blacknose shiner	*Pimephales notatus* bluntnose minnow	*Pimephales promelas* fathead minnow	*Semotilus atromaculatus* creek chub	*Semotilus corporalis* fallfish
Crow						1			
Eagle	7					16			
Little Green		411				20			
Mazinaw									
Palmerston						70			
Shabomeeka						1			
Silver					91				
Mair	34					47	10		
Mosque	99					136	21		3
Cronk	90					31			
Egg	220	895	8	44		115	197		
Granite	5					424	15	5	
Grindstone						32			
Otter	4	2				3			
Upper Rock	12					126			
White						9			
13 Island	60					350			
Flower Round		1							
Hambly	19								
Joe's									
Upper Park	36	6				32			
Sand (Bedford)	4					26			
Sand (Plevna)	9					157			
Black	114			5		2			
Buckshot						6			
Otty					35	2			
Patterson	66			45		68			
Pike		11			65				
Red Horse	3					166			
Robertson	2					10			
St George		13				6			

Appendix 7. Criteria for selection of fish species included in planktivorous fish variables. Note, selection criteria do not pertain to young-of-the-year fish as they were excluded from the analysis due to methodological problems (see methods).

Fish species	included in index (X)	comments (as per Scott and Crossman 1973)
Lepomis spp.		omnivore
Ambolites rupestris		omnivore
Micropterus spp.		piscivore
Pomoxis nigromaculatus		omnivore
Catostomus commersoni		detritivore
Ictalurus nebulosus		omnivore
Perca flavescens	X	planktivore (when total length < 10 cm)
Stizostedion vitreum		piscivore
Etheostoma exile	X	planktivore
Percina caprodes	X	planktivore
Esox lucius		piscivore
Umbra limi	X	planktivore
Fundulus diaphanus	X	planktivore
Labidesthes sicculus	X	planktivore
Phoxinus eos	X	planktivore
Couesius plumbeus	X	planktivore
Hybognathus nuchalis	X	planktivore
Notemigonus crysoleucas	X	planktivore
Notropis spp.	X	planktivore
Pimephales spp.	X	planktivore
Semotilus spp.	X	planktivore