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TO MY HUSBAND, IAIN

(NAPOLEON & WELLINGTON)

AND MY PARENTS.

Any 'school of thought' too aggressively defended tells us more of human insecurity than the operation of ecosystems.

-Brian Moss, Ecology of Freshwater: Man and Medium

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TABLE OF CONTENTS

Acknowledgements i

Table of Contents ii

Abstract iv

Résumé vi

List of Figures ix

List of Tables xi

Introduction 1

Methods 12

  Study Area 12

  Sampling 16

  Laboratory 17

    A. Morphometric Factors 17

    B. pH and Alkalinity 17

    C. Total Phosphorus 17

    D. Chlorophyll a 17

    E. Zooplankton 19

      i. Biomass 19

      ii. Size Structure 20

    F. Fish Composition 20

Statistical Methodology 22

TABLE OF CONTENTS- CONTINUED

Results 25
    Bottom-Up Relationships 26
    Top-Down Relationship 28
    Trophic Status and Top-Down Effects 31
Discussion 80
General Conclusion 86
Literature Cited 87
Appendix A 93
Appendix B 94
Appendix C 96
Appendix D 97
Appendix E 98
Appendix F 99
Appendix G 100

ABSTRACT

It has been hypothesized that the trophic structure of aquatic ecosystems is controlled by two sets of processes, often referred to as bottom-up and top-down. The bottom-up hypothesis postulates that nutrient limitation, and various physical-chemical factors directly or indirectly regulate the biomass and community structure of organisms at all levels of the food web. Whereas the top-down hypothesis postulates that predation by upper levels of the food web (specifically piscivorous fish) strongly influence the biomass, community size structure and productivity of organisms in the lower trophic categories. Further, it has been proposed that the effect of predation might be mediated by the trophic status or richness of a lake. That is, top-down forces are more pronounced in oligotrophic systems. In this study we attempt to determine the strength of both bottom-up and top-down control on lower trophic level biomass and community size structure, specifically zooplankton and phytoplankton, in lakes of varying trophic status.

During summer stratification, 29 temperate lakes of varying trophic status and fish species composition were sampled in Québec and Ontario. Morphometric, chemical and biological parameters were measured.

This study found a strong relationship between nutrient availability and phytoplankton biomass, and between nutrient availability and zooplankton size structure. Bottom-up effects were quite strong at both the phytoplankton and zooplankton levels.

Neither piscivorous fish presence nor indices of piscivorous fish abundance had a detectable effect on most indices of phytoplankton and zooplankton biomass and community size structure. Only cladoceran biomass and the variance in individual dry weight were higher in lakes where piscivorous fish were present. Piscivorous fish predation-effects were not evident at the phytoplankton level and were relatively weak at the zooplankton level.

Additionally, total zooplankton biomass, crustacean biomass and cladoceran biomass were significant in explaining residual variation in the TP-Chl *a* model and in turn improved this model's predictive ability by 24 %, 18 % and 22 %, respectively.

Finally, this study found that the effect of piscivorous fish did not depend on the concentration of total phosphorus in the 29 lakes. Thus, no evidence of interaction between trophic status and predation was determined.

RÉSUMÉ

L'hypothèse que la structure trophique des écosystèmes aquatiques est contrôlée par deux séries de processus appelés incidences ascendantes et incidences descendantes a été émise.

L'hypothèse des incidences ascendantes postule que la limitation en éléments nutritifs ainsi que divers facteurs physico-chimiques influencent directement ou indirectement la biomasse et la structure de communauté, et ce, à tous les niveaux de la chaîne alimentaire.

L'hypothèse des incidences ascendantes postule que la prédation par des organismes situés plus haut dans la chaîne alimentaire (particulièrement les poissons piscivores) influence fortement la biomasse, la structure en taille de la communauté et la productivité des organismes situés à des niveaux trophiques inférieurs. Plus tard, il a été proposé que la trophie ou la richesse d'un lac pouvait servir d'intermédiaire à l'effet de la prédation. Donc, les forces descendantes sont plus prononcées en milieu eutrophe.

Dans cette étude, nous tentons de déterminer l'ampleur des forces ascendantes et descendantes sur la biomasse et la structure en taille des niveaux trophiques inférieurs (en particulier le zooplancton et le phytoplancton pour des lacs aux statuts trophiques variés.

Nous avons échantillonné 29 lacs variant en statuts trophiques ainsi qu'en composition d'espèces de poissons.

Les paramètres morphométriques, chimiques et biologiques ont été mesurés.

Nous avons trouvé une forte relation entre la disponibilité des éléments nutritifs et la biomasse du phytoplancton et entre la disponibilité des éléments nutritifs et la structure en taille du zooplancton.

Les incidences ascendantes étaient assez marquées aux niveaux du phytoplancton et du zooplancton.

Ni la présence de poissons piscivores, ni l'indice d'abondance de poissons piscivores n'a d'effet significatif sur la plupart des indices de biomasse et de structure en taille du phytoplancton et du zooplancton.

Seul la biomasse des cladocères et la variance dans le poids sec individuel étaient plus élevées dans les lacs où les poissons piscivores étaient présents.

Les effets de la prédation par les poissons piscivores n'étaient pas notables au niveau du phytoplancton et relativement faibles au niveau du zooplancton.

De plus, la biomasse du zooplancton total, la biomasse des crustacés et la biomasse des cladocères étaient significatifs pour l'explication de la variation résiduelle du modèle TP-Chla et amélioraient la capacité de prédiction de ce modèle par 24%, 18%, et 22% respectivement.

Finalement, nous avons trouvé que, pour les 29 lacs, l'effet des poissons piscivores ne dépendait pas de la concentration du phosphore total. Donc,

aucune évidence d'interaction entre le statut trophique et la prédation n'a été observée.

LIST OF FIGURES

FIGURE 1- Location of 29 sampling sites 15

FIGURE 2- The relationship between log summer total chlorophyll *a* concentration and log summer total phosphorus concentration in the 29 lakes 43

FIGURE 3- The same relationship as Figure 2 including a dashed line representing the regression model of Dillon and Rigler (1974) 45

FIGURE 4- The relationship between log mean summer zooplankton biomass and log mean summer total phosphorus concentration including a dashed line representing the regression model of Pace (1986) 47

FIGURE 5- The relationship between log mean summer zooplankton biomass and log mean summer total chlorophyll *a* concentration in the 29 lakes . . . 49

FIGURE 6- The relationship between log mean summer crustacean biomass and log mean summer total phosphorus concentration in the 29 lakes 51

FIGURE 7- The relationship between log mean summer crustacean biomass and log mean summer total chlorophyll *a* concentration in the 29 lakes . . . 53

FIGURE 8- The relationship between log mean summer cladoceran biomass and log mean summer total phosphorus concentration in the 29 lakes 55

FIGURE 9- The relationship between log mean summer cladoceran biomass and log mean summer total chlorophyll *a* concentration in the 29 lakes . . . 57

FIGURE 10- The relationship between mean individual zooplankton dry weight and log mean summer total phosphorus concentration in the 29 lakes 59

FIGURE 11- The relationship between mean individual zooplankton dry weight and log mean summer total chlorophyll *a* concentration in the 29 lakes . . . 61

FIGURE 12- The relationship between variance of individual zooplankton dry weight and log mean summer total phosphorus concentration in the 29 lakes 63

FIGURE 13- The relationship between variance of individual zooplankton dry weight and log mean summer total chlorophyll *a* concentration in the 29 lakes65

FIGURE 14- The effect of piscivorous fish presence or absence on zooplankton biomass and size structure in the 29 lakes 67

FIGURE 15- The effect of piscivorous fish presence or absence on phytoplankton biomass and size structure in the 29 lakes 69

FIGURE 16- The relationship between the TP-Chl a (log total phosphorus concentration vs. mean log total chlorophyll *a* concentration) residuals and the TP-ZB (log total phosphorus concentration vs. mean log total zooplankton biomass) residuals in the 29 lakes 71

FIGURE 17- The relationship between the TP-Chl *a* (log total phosphorus concentration vs. mean log total chlorophyll *a* concentration) residuals and the TP-CRB (log total phosphorus concentration vs. mean log total crustacean biomass) residuals in the 29 lakes 73

FIGURE 18- The relationship between the TP-Chl *a* (log total phosphorus concentration vs. mean log total chlorophyll *a* concentration) residuals and the TP-CLB (log total phosphorus concentration vs. mean log total cladoceran biomass) residuals in the 29 lakes 75

FIGURE 19- The relationship between the TP-Chl *a* (log total phosphorus concentration vs. mean log total chlorophyll *a* concentration) residuals and the TP-MDW (log total phosphorus concentration vs. mean individual zooplankton dry weight) residuals in the 29 lakes 77

FIGURE 10- The relationship between the TP-Chl *a* (log total phosphorus concentration vs. mean log total chlorophyll *a* concentration) residuals and the TP-VDW (log total phosphorus concentration vs. variance in individual zooplankton dry weight) residuals in the 29 lakes 79

LIST OF TABLES

TABLE 1- List of 29 sample lakes including their location, total phosphorus concentration and presence or absence of piscivorous fish 32

TABLE 2a- The range of morphometric and physico-chemical encountered in the 29 sample lakes 33

TABLE 2b- Description and range of untransformed limnological variables measured in this study 34

TABLE 3a- Summary of simple linear regression statistics for log chlorophyll *a* concentration, log zooplankton biomass, log crustacean biomass, log cladoceran biomass, mean individual zooplankton dry weight and variance of individual zooplankton dry weight using log total phosphorus concentration and log chlorophyll *a* concentration as an independent variable 35

TABLE 3b- Summary of second order polynomial regression examining the effect of log total phosphorus and (log total phosphorus)^2 on log chlorophyll *a* concentration in the 28 lakes 36

TABLE 3c- Summary of third order polynomial regression examining the effect of log total phosphorus, (log total phosphorus)^2 and (log total phosphorus)^3 on log chlorophyll *a* concentration in the 28 lakes 36

TABLE 4a- Summary of results of One-Way ANOVA models for log chlorophyll *a* concentration, log zooplankton biomass, log crustacean biomass, log cladoceran biomass, mean individual zooplankton dry weight and variance of individual zooplankton dry weight using fish presence or absence as the independent variable 37

TABLE 4b- Summary of Spearman rank correlations between log piscivorous fish abundance index and log chlorophyll *a* concentration, log zooplankton biomass, log crustacean biomass, log cladoceran biomass, mean and variance in individual zooplankton dry weight for 18 lakes 37

TABLE 4C- Summary of an analysis of covariance model for log chlorophyll *a* concentration using fish presence or absence, size class and the interaction term as the independent variables 38

TABLE 5- Summary of partial correlations, after controlling for log total phosphorus, between log chlorophyll *a* concentration, log zooplankton biomass, log crustacean biomass and log cladoceran biomass and the two indices of zooplankton community structure 38

TABLE 6- Summary of three multiple regressions examining the effect of log total phosphorus concentration and log zooplankton biomass, log crustacean biomass and log cladoceran biomass on log chlorophyll a concentration for 28 lakes 39

TABLE 7- Summary of ANCOVA models examining the effect of log total phosphorus concentration and the presence or absence of piscivorous fish on log chlorophyll *a* concentration, log zooplankton biomass, log crustacean biomass, log cladoceran biomass, mean and variance in individual zooplankton dry weight in 28 lakes 40

INTRODUCTION

The factors governing the structure of natural food webs have been the subject of intense study for several decades (Hairston *et al.*, 1960; Hrbáček, 1962) for reasons of both fundamental and practical interest. Bottom-up models of ecosystem trophic structure have suggested that nutrient availability determines plant growth and abundance, which in turn determines herbivore growth and abundance, and so on, up the food web (Harris, 1986). Top-down models (Carpenter *et al.*, 1985; Carpenter and Kitchell, 1987) have emphasized the effect of predators on lower trophic levels. For example, it has been suggested that the world is green because carnivores prevent herbivores from fully exploiting plant biomass (Hairston *et al.*, 1960).

In aquatic systems, bottom-up models have received the most attention. These models suggest that the pelagic food web is ultimately controlled by the producers, hence nutrient limitation both directly and indirectly regulates all trophic levels. Research has concentrated on these models for two principle reasons: firstly because significant statistical relationships have been found between the total phosphorus concentration in lake water and the biomass of most groups of aquatic organisms (Prairie *et al.*, 1989; Peters, 1986), and secondly because experimental results have linked artificial increases in nutrient loading to increased phytoplankton biomass (Schindler, 1974; 1978). Sakamoto (1966) first demonstrated the strong empirical relationship between total nitrogen, total phosphorus and chlorophyll concentration in Japanese lakes. This relationship was also observed by Dillon and Rigler (1974) who found a significant TP-Chl relationship in 19 Canadian lakes. The lakes were chosen to vary in as many ways and as widely as possible, particularly in their nutrient loads. The extent of producer control was evaluated by using total phosphorus as a measure of nutrient availability and total chlorophyll *a* as a measure of phytoplankton standing crop. The strong resulting regression suggests that nutrient availability is an important factor in determining phytoplankton biomass.

This type of analysis has been repeated in over 60 different published studies in various regions (Peters, 1986). In all cases significant linear relationships have been found between phosphorus and chlorophyll *a*. Most report a log-log linear regression of the form:

$$\log(\mathrm{Chl}\,a) = b_0 \log(P) + b_1$$

However, McCauley *et al.* (1989) and Prairie *et al.* (1989) proposed that in fact the relationship is sigmoidal, and it would be better modelled by a polynomial or non-linear regression. Essentially, they submitted that the above relationship often appears to be linear because only a narrow range of phosphorus values has been examined. At low phosphorus concentrations (< 50 µg litre^{-1}) lakes are sensitive to phosphorus loading, but a saturation point is eventually reached whereby another variable becomes limiting. It should be noted that although the authors propose an alternative mathematical model, the strong relationship between phosphorus and phytoplankton biomass is not in doubt.

The nature of the phosphorus-phytoplankton relationship has been investigated in great detail using manipulative techniques. One of the most comprehensive of these is the series of ecosystem experiments at the Experimental Lakes Area (ELA) of northern Ontario. These experiments included large scale (i.e. whole lake) manipulations. They demonstrated that a change in nutrient loading resulted in a subsequent change in lake productivity (Schindler, 1974; 1978). Essentially, they determined that phosphorus sets the limit to biotic productivity in temperate zone lakes. As in the comparative studies above, the analysis can be summarized in the form of a regression between TP and Chl *a*.

Taken together, this body of research provides great support for the bottom-up model. However, there are some significant issues that remain unresolved. Firstly, the vast majority of the literature concentrates only on producer control at the bottom of the food web. While the relationship between nutrients and phytoplankton has been well established similar relationships between nutrients and zooplankton, phytoplankton and zooplankton, zooplankton and planktivorous fish, and planktivorous and piscivorous fish have been studied in much less detail. However, a few such bottom-up relationships have been observed (see for instance Pace, 1986; Bays and Crisman, 1983;

McCauley and Kalff, 1981; Hanson and Leggett, 1982; Downing et al., 1990).

Although many authors have found significant regressions between total phosphorus and chlorophyll *a*, there are large portions of the variability in chlorophyll *a* which are unexplained by nutrient loading (Prairie, *et al.*, 1989). In fact, algal biomass and productivity in lakes with similar nutrient supply rates can differ nearly three orders of magnitude (Carpenter *et al.*, 1985; Carpenter and Kitchell, 1987).

It has been suggested that fish predation may be important in explaining the remaining residual variability in productivity in aquatic pelagic systems (Carpenter *et al.*, 1985; Carpenter and Kitchell, 1987). Top-down effects were first described by Hrbácěk *et al.* (1961) . In their study, they demonstrated an impact of planktivorous fish on the amount and composition of the zooplankton community and in turn the phytoplankton community. These observations were later formalized by Brooks and Dodson (1965) in the size efficiency hypothesis. This hypothesis maintains that large zooplankton are more efficient at processing their food and, in the absence of planktivorous fish, will competitively eliminate the smaller species of zooplankton. But, as the intensity of planktivory increases, larger zooplankton will be selectively eliminated and smaller zooplankton will begin to dominate. However, at an intermediate level of planktivory, both large and small zooplankton populations are present. The observations of Hrbácěk *et al.* (1962) and the size efficiency hypothesis stimulated a large amount of research into top-down effects in aquatic pelagic food webs in the past 20 years. In fact, the debate has recently shifted from the existence of top-down effects to their quantification.

Carpenter, *et al.* (1985) suggested that fluctuations in piscivory might cascade through the aquatic food web initiating changes in planktivory, herbivory and primary production. This hypothesis of "cascading trophic interactions" arose out of the earlier observations of Hrbáček *et al.* (1962) and the unexplained differences in productivity among lakes with similar nutrient supplies. In particular, Carpenter *et al.* (1985) considered a study by Schindler (1978) in which 66 phosphorus-limited lakes were sampled. In these lakes 48% of the variability in productivity could be statistically explained by nutrient loading. However, when the nutrient effects were statistically removed, productivities still varied a hundredfold. When the additional variability due to climate and methodology were removed, the productivities still varied tenfold (Carpenter *et al.* 1985; Carpenter and Kitchell, 1987). According to Carpenter *et al.* (1985) the cascading trophic interactions that are transmitted down through the food web could cause the remaining variance in phytoplankton biomass and production at constant nutrient loads.

The cascading trophic interaction hypothesis assumes four trophic levels: 1) piscivorous fish such as bass, pike and trout, 2) planktivorous fish or invertebrate planktivores, 3) zooplankton, and 4) phytoplankton (Carpenter *et* *al.*, 1985). In terms of these levels the specific predictions of the model are:

1. Increased piscivorous fish density results in decreased planktivorous fish density and species composition. Thus, an increase in the abundance of piscivorous fish reduces planktivorous fish abundance.

2. A decrease in planktivorous fish abundance allows large bodied herbivorous and predacious species to dominate the zooplankton community. The density of large crustaceans, particularly Daphnia species,increases.

3. Large herbivorous zooplankton alter the biomass, species composition and size structure of phytoplankton directly by selective grazing and indirectly through nutrient recycling. Increased rates of herbivory lead to lower phytoplankton biomass and dominance by large, inedible algal species (Post and McQueen, 1987; Carpenter *et al.* 1985).

Various experiments have examined these predictions both separately and as a whole. The negative relationship between piscivorous fish and planktivorous fish has been demonstrated quantitatively in studies using both enclosures and manipulated ponds (Holcik, 1977; Bonar, 1977; Hambright *et al.*, 1986; McQueen *et al.*, 1990). The prediction which has probably received the most attention is the effect of planktivorous fish abundance on zooplankton biomass and size structure (Hrbáček, 1962; Hall *et al.*, 1970; Leah *et al.*, 1980; Mills *et al.*, 1987; Lynch, 1979; Lynch and Shapiro, 1981; McQueen and Post, 1988). All of these studies found a significant relationship between planktivorous fish abundance and zooplankton biomass and size structure. However, fewer studies have demonstrated an inverse relationship between zooplankton and phytoplankton abundance (Carpenter *et al.*, 1985; Lynch, 1979; Lynch and Shapiro, 1981; Levitan *et al.*, 1985). These top-down studies have all been relatively short, ranging in length from 40 days to 1 year. Moreover, several studies (some of which have been in progress for more than 9 years) have failed to observe reduced phytoplankton biomass due to top-down effects (Hall *et al.*, 1970; Vijverberg and Van Densen, 1984; Lammens, 1988; Lehman, 1988; Benndorf *et al.*, 1988; Drenner *et al.*, 1986; McQueen and Post, 1988; Post and McQueen, 1987; McQueen *et al.*, 1990).

The practical applications of this top-down theory are biomanipulation strategies such as those proposed by Shapiro *et al.* (1975). These strategies attempt to decrease algal abundance by artificially increasing the top predators in pelagic systems (Shapiro and Wright, 1984; Lynch and Shapiro, 1981). This technique has been suggested as a cost-effective alternative to nutrient abatement as a means of controlling nuisance algal growth, where diffuse nutrient inputs occur or efficient internal cycling makes it impossible to diminish nutrient availability through the reduction of point sources (Carpenter and Kitchell, 1992).

Biomanipulation has had mixed results. An apparently successful example of biomanipulation is Lake Michigan, in which an aggressive salmonine stocking program was followed by significant improvements in water quality (Scavia *et al.*, 1986). However, recently Evans (1992) disputed these results based on a consideration of long-term historical data. As well, other whole lake and enclosure studies have shown little effect of fish manipulation on phytoplankton abundance (Post and McQueen, 1987). Moreover, in Lake Ontario, chlorophyll levels have not changed in response to a salmonine stocking program similar to that in Lake Michigan (Lean *et al.*, 1990).

It is not clear why top-down effects are observed in some cases but not others. McQueen *et al.* (1986) proposed that predator-prey interactions are strongest at the top of the aquatic pelagic food but progressively weaken with each additional trophic step from the top predator, whereas nutrient control weakens with each step up the food chain. That is, top-down effects of piscivorous fish will always be strongest on planktivorous fish, whereas nutrient effects are strongest on total chlorophyll *a*. However, other relationships in the middle of the food web will be less significant.

This theory is supported by a comprehensive enclosure study (nine years) (McQueen, *et al.*, 1990) that revealed no long term effects of piscivorous fish on total chlorophyll *a*. Their regressions based on annual means demonstrated that piscivore abundance had a strong negative significant impact on planktivore abundance, however planktivores had no significant impact on zooplankton size structure or biomass, and most importantly fish, both piscivore and planktivore, did not significantly alter chlorophyll *a* concentrations. But, as in many other studies, a positive significant correlation was obtained between chlorophyll *a* and total epilimnetic phosphorus. This particular study lends support to the hypothesis of McQueen *et al.* (1986) that at the top of the food chain top-down forces are strongest, whereas at the bottom of the food chain phytoplankton biomass is strongly dependent on bottom-up effects.

McQueen *et al.* (1986) further suggest that the extent of dampening depends on the trophic status of the lake. They hypothesize that in eutrophic lakes top-down effects are strong from piscivorous fish to planktivorous fish, somewhat weaker for planktivorous fish to zooplankton and have little impact for zooplankton to phytoplankton because only large bodied zooplankton have a significant impact on phytoplankton biomass. However, in oligotrophic lakes these top-down effects are not well buffered, and zooplankton to phytoplankton interactions are strong because zooplankton of all sizes impact phytoplankton biomass. This theory has been supported by a study comparing the trophic interactions in a oligotrophic lake to those in an eutrophic lake (LaFontaine and McQueen, 1992).

Variability in the results of top-down studies might also be because of the short-term effects of predator manipulation. Further, many studies have employed sledgehammer manipulations of piscivores and planktivores (all or none), and often unrealistic fish densities. Thus, the question arises: do these studies represent natural systems? It is possible that extreme manipulations may produce statistically significant changes in plankton abundance but may not reflect conditions found in nature.

The purpose of this research is to examine the relationship between the presence or absence of piscivorous fish, as well as an index of fish abundance and both zooplankton and phytoplankton biomass and community size structure in 29 unmanipulated lakes. These lakes were selected to represent a range of morphometric, chemical and trophic conditions, and they were then classified based on the presence or absence of piscivorous fish. These lakes presumably contain plankton communities that are more or less at equilibrium with their fish communities.

There have been few studies examining the natural (as opposed to manipulated) variation of lower trophic levels in temperate zone lakes while addressing Carpenter and Kitchell's (1985) top-down predictions. In this study we intend to do so. We will also test McQueen's (1986) hypothesis that top-down effects are mediated by trophic status. Additionally, this study will determine the relative importance of bottom-up effects versus top-down effects on lower trophic levels structure.

The following predictions of the bottom-up hypothesis were tested:

Total chlorophyll *a* concentration is positively correlated with total phosphorus concentration as they covary among lakes; zooplankton biomass is positively correlated with total chlorophyll *a* concentration; zooplankton biomass is also positively correlated with total phosphorus concentration, but less strongly so than with chlorophyll *a* concentration; zooplankton community size structure is dependent on total phosphorus concentration and chlorophyll *a* concentration.

Then, the following predictions of the top-down hypothesis were addressed:

After controlling for variations in total phosphorus concentration, zooplankton biomass is higher in lakes having piscivorous fish than in lakes without piscivorous fish. Consequently, phytoplankton biomass is lower in lakes having piscivorous fish than in lakes without piscivorous fish. Lakes with piscivorous fish have larger sized zooplankton, and larger sized, inedible phytoplankton than in lakes without piscivorous fish.

Finally, McQueen's hypothesis (1986) that top-down interactions are buffered in richer lakes will be addressed by testing the interaction between total phosphorus concentration and piscivorous fish presence.

METHODS

STUDY AREA

A total of 29 lakes in eastern Ontario and western Quebec were sampled during the summer of 1991. The lakes were selected to represent a range in trophic status, fish composition and morphometry. Since the purpose of this study was to examine the differences among lakes and not within given lakes, the sampling method concentrated on the inter-lake variation. Each of the lakes (except two) was sampled twice during summer stratification from June 10 to September 11.

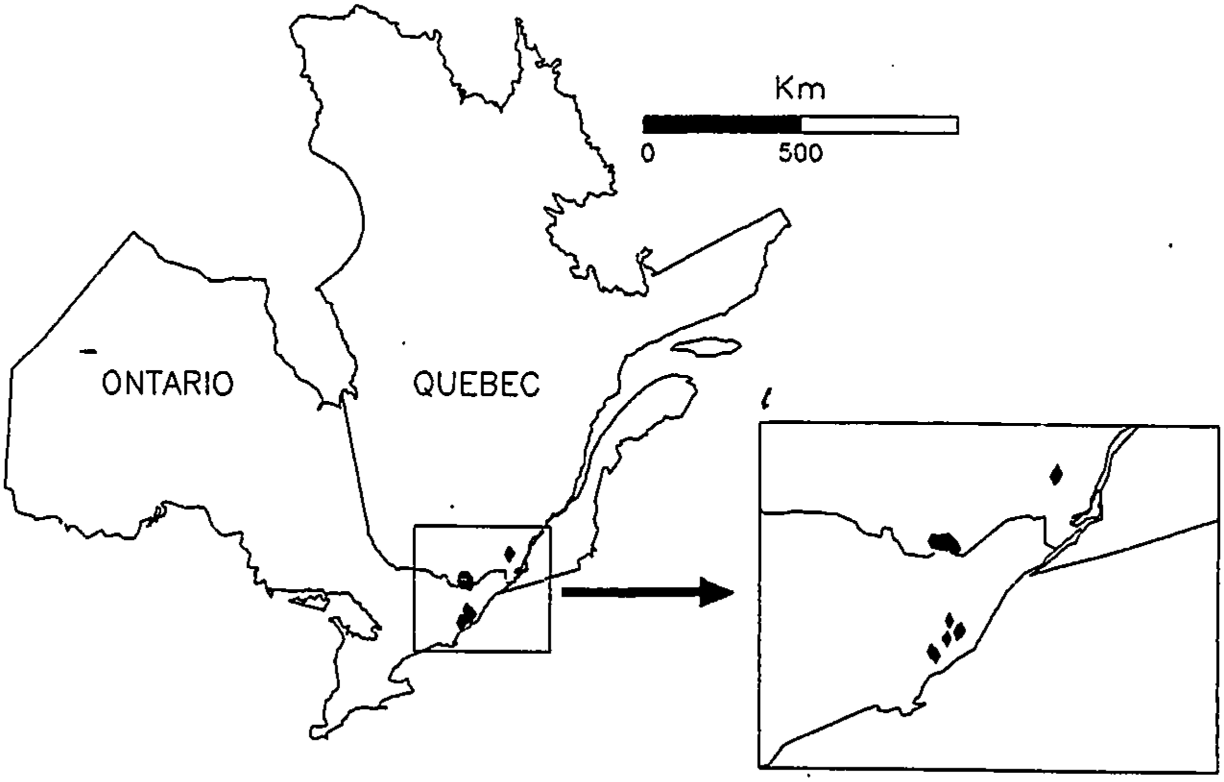
Of the 29 lakes sampled, 18 (Black, Brown, Carmen, Fortune, Harrington, Kidder, Kingsmere, La Pêche, Le Blanc, Loutre, Meech, Mulvihill, Petit Renaud, Philippe, Ramsey, Renaud, Taylor, Vase) are found in Gatineau Park, a protected area spanning 35 000 hectares, located between the Ottawa and Gatineau Rivers. The main tree species bordering these lakes are *Pinus* spp. and *Acer* spp.

Five of the 29 lakes (Croche, Cromwell, Geai, Pin Rouge, Triton) sampled are located in the Laurentians near St. Hippolyte, Québec approximately 80 km north of Montreal, on the Laurentian Shield. Four of these lakes (except Pin Rouge) are on the Université de Montréal research station property. The most common tree species bordering these lakes is the white birch, *Betula papyrifera*.

The remaining six lakes (Big Rideau, Gould, Lower Beverley, Opinicon, Sydenham, Upper Beverley) are in Rideau lake district of southeastern Ontario, near Kingston. All six are relatively large with active sport fisheries, and are located in a well developed cottage area.

See Figure 1 and Appendix A for map of study sites and their coordinates.

Figure 1- Location of sampling sites in this study. Twenty-nine lakes were sampled in Ontario and Québec. Refer to Appendix for latitude and longitude coordinates.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QUEBEC

SAMPLING

For small- and moderate-sized lakes, samples were taken at the centre of the lake. For larger lakes, samples were taken off-shore at depths no greater than 15 m. The following physical characteristics were determined: depth, Secchi depth, epilimnion depth, conductivity (with a YSI salinity-conductivity-temperature metre) and dissolved oxygen (YSI oxygen meter). The site depth was established using a calibrated rope to the nearest 0.25 m. The epilimnion depth was taken as the point of inflexion in the temperature profile.

Integrated epilimnetic water samples were taken using an 8 m length of 2.5 cm diameter Tygon tubing. These water samples were returned to the laboratory and analyses were begun within 4 hours. A subsample of each of these bottles was used to determine total phosphorus (TP), chlorophyll *a* (CHL *a*), pH, and alkalinity.

Integrated zooplankton samples were taken using a diaphragm pump connected to a hose 2.5 cm in diameter. The hose was drawn repeatedly through the water column from 0.5 m above the bottom to the surface. The outflow was passed through a 35-μm nitex net to gather the macrozooplankton. The zooplankton were then transferred to a small container and preserved in sucrose-formalin solution with a final concentration of 4% formalin (Haney and Hall, 1975). The volume of water thus sampled was calculated from the pumping rate (25 l min^{-1}) and the time of pumping.

LABORATORY

A. Morphometric Factors

Morphometric variables such as lake surface area, mean depth, maximum depth, were obtained from various published sources (NCC, 1981-1983; Lafond *et al.*, 1990; MOE, 1984; 1985).

B. pH and Alkalinity

The pH of each lake was determined using a Corning pH meter, and the alkalinity was estimated by titrating 100-mL of lake water with 0.1 N HCL to pH 3.5 (Wetzel and Likens,1991). A linear regression of pH as a function of acid added was calculated for pH measurements between 4.5 and 3.5. This regression was used to extrapolate to the equivalence point (i.e. the point at which proton accumulation is proportional directly to the titrant added). The alkalinity was then computed as the number of microequivalents of acid required to reach the equivalence point, divided by the sample volume (100 ml).

C. Total Phosphorus

Quadruplicate 50-mL subsamples were digested with potassium persulfate under 15 psi of pressure for 40 minutes, then analyzed using the molybdenum blue method of Menzel and Corwin (1965). The water samples were not prefiltered to remove larger particles.

D. Chlorophyll *a*

Size-specific filtration of phytoplankton was used. Total chlorophyll *a* concentration was determined by filtering 250-500 mL of lake water on a Whatman GF/F filter under low vacuum pressure. Net chlorophyll *a* concentration was determined by filtering 1 L of lake water on a 35 μm nitex filter. The filtrate from the 35 μm filter was then passed through a 12 μm polycarbonate filter (Poretics corporation, Livermore, California). Similarly, the 12 μm filtrate was filtered on a 2 μm polycarbonate filter. Finally, 250 mL of the last filtrate was filtered on a 0.2 μm polycarbonate filter. These filters were then frozen. Chlorophyll *a* was extracted in 95% ethanol for approximately 24 hrs, and then assayed spectrophotometrically (Ostrofsky and Rigler, 1987). A corrected version of their calibration equation was used to estimate chlorophyll *a* concentration (Ostrofsky, pers. comm.).

$$-\text{Chl A} = \frac{(13.7\ A_{665} - 5.76\ A_{649})\ v}{V^{*}l}$$

where:

Chl *a* is chlorophyll *a* concentration in ug/L

A_{665} is the corrected optical density at 665nm

A_{649} is the corrected optical density at 649nm

v is the volume of the extractant used in mL

V is the volume of lakewater filtered in litres

l is the light path of the cuvette in cm.

E. Zooplankton

The preserved zooplankton samples were sub-sampled to reduce the number of organisms that would be counted and measured. A modification of the Huntsman Marine Laboratory (HML) technique (Van Guelphen *et al.* 1982) was used. Each sample was diluted to 1 L using tap water. The sample was then split into quarters by pouring small amounts alternately into each of four beakers (while stirring) until each beaker contained 250 mL. To obtain a smaller subsample the procedure was repeated using one of the four beakers chosen at random. When the necessary subsample was obtained, it was filtered through a 35um nitex filter. The collected zooplankton were then washed into a disposable plastic centrifuge tube using 10% formalin-sucrose.

i. Biomass

To determine zooplankton biomass for each lake, one of the subsamples generated above was examined using a microscope and a micro-computer based caliper system (Sprules *et al.* 1981). Between 100-200 individuals were counted for each lake. The individuals were classified into one of four groups: cladoceran, copepod, naupli, and rotifer. The length of each individual was measured and recorded. Biomass was determined using the general mass-length regression for zooplankton proposed by Peters and Downing (1984):

$$W=9.85*L^{2.1}$$

where, Dry Body Weight (μg) and L=length (mm)

ii. Size structure

The first two moments (mean and variance) of the distribution of the log-transformed biomasses were determined for each of the four groups (i.e. cladocerans, copepods, nauplii, rotifers) in each lake. Because a different sub-sample fraction was used for each group, it was necessary to perform a weighting procedure based on sample volume to obtain the mean and variance of the cumulative distribution of log zooplankton biomass from the group means and variances (see Appendix B for details).

G. Fish Composition Data

The fish community data for the lakes located in Gatineau Park were provided by by Dr. François Chapleau (University of Ottawa, pers. comm.). Dr. Alan Keast (Queen's University, Department of Biology, pers. comm.) provided fish community data for Opinicon, Gould, Lower Beverley, Upper Beverley, Sydenham and Big Rideau. Dr. Daniel Boisclair (Université de Montréal, Département de Sciences Biologiques, personal communication) provided fish community data for Croche, Cromwell, Triton, Geai and Pin Rouge.

For the non-Gatineau lakes, detailed data on fish abundance and composition were not available. Rather, it was only possible to determine piscivorous fish presence/absence. In Gatineau Park, an estimate of abundance was obtained on 18 lakes.

The Gatineau data were collected between May and August over a three year period (1989-1991). The equipment used included: two experimental gill nets (40 X 1.8 m with mesh panels of 13, 19, 25, 31, 38 mm); a trammel net (37 X 1.2 m with outer mesh panels of 20 cm and inner mesh of 25 mm); two trap nets (9.1 X 0.9 m with mesh panels of 6 mm and rings 76 cm in diameter); a 10 m seine and finally 18 unbaited minnow traps (44.5 cm long, 23 cm in diameter with a 1.1 cm opening). All the stationary gear remained in the lake for 48 hrs, however the gill nets and trammel net were checked after 24 hrs and the fish were removed. The fish caught were identified, counted and most were returned to the lake, while some were retained for permanent preservation and future record (Szenasy, Chapleau and Findley, unpublished). An index of piscivorous fish abundance was calculated using the total catch of piscivorous fish/48 hr in trammel, gill and seine nets. As *Perca flavescens* can be both planktivorous and piscivorous at different periods in its life cycle, fish greater than 100 mm were considered piscivorous, whereas those smaller were considered planktivorous.

STATISTICAL METHODOLOGY

The variables used throughout the statistical analyses are: the logarithm of total phosphorus concentration (log TP), logarithm of total chlorophyll *a* concentration (log Chl *a*), logarithm of total zooplankton biomass (log ZB), logarithm of total crustacean biomass (log CRB), logarithm of total cladoceran biomass (log CLB), the mean of the logarithm of individual dry weight of zooplankton (MDW), the variance of the logarithm of individual dry weight of zooplankton (VDW), the logarithm of the index of piscivorous fish abundance (log PFA), a categorical variable denoting presence (1) or absence (0) of piscivorous fish (PFISH) and a categorical variable denoting chlorophyll *a* size class (SIZE). The variables were log transformed in the analyses in order to stabilize the variances and satisfy the assumptions of normality and homoscedasticity. The categorical variables remain untransformed.

The simple relationships between continuous variables were examined by means of simple linear regression. log ZB, log CRB, log CLB, MDW and VDW were each regressed against log TP and log Chl *a*. Second and third degree polynomial regressions using log TP, log TP^2 and log TP^3 as independent variables and log Chl *a* as the dependent variable were examined.

The effect of piscivorous fish (PFISH) presence on log Chl *a*, log ZB, log CRB, log CLB, MDW, VDW was assessed by conducting ANOVA's. Spearman Rank correlations were calculated between log PFA and the following variables:

log Chl *a*, log ZB, log CRB, log CLB, MDW and VDW.

Partial correlations were used to examine the relationship between log Chl *a* and log ZB, log CLB, log CRB, MDW and VDW, while controlling for log TP, in order to determine how much of the residual variability in the log TP-log Chl *a* might be explained by other variables. Those variables found to be significant in these correlations where then used as independent variables, along with log TP, in multiple regressions with log Chl *a* (dependent variable).

To test the effect of PFISH on phytoplankton SIZE class, an ANCOVA was used. This test included the following independent variables: PFISH, SIZE and PFISH*SIZE. In this test SIZE was a four level categorical variable denoting log Chl *a* size class (1= Pico; 2= Nano; 3= Micro; 4= Net).

To test the combined effects of PFISH and log TP on log Chl *a*, log ZB, log CRB, log CLB, MDW, VDW, an ANCOVA with PFISH (categorical), log TP (continuous), and PFISH*log TP (interaction term) as independent variables was used.

Zooplankton biomass in one lake, Petit Renaud, proved to be an order of magnitude lower than in any other lake. It was therefore decided to test if Petit Renaud was an outlier and should be removed from the statistical analysis. This determination was based on a standard outlier rejection test in which the following t-statistic is calculated:

$$t = (X\text{-}Xi) / \sigma$$

where X is the mean of all samples, X_i is the mean of Petit Renaud and σ is the standard deviation of all samples, including suspected outliers. This statistic was calculated for log ZB, log CRB and log CLB and the results are presented below. The null hypothesis for this test is that Petit Renaud is drawn from the same population as the other 29 sample lakes. This hypothesis was rejected in each case. Thus, Petit Renaud was removed as an outlier point. The mean individual mass of zooplankters in Petit Renaud fell within the values observed in other lakes; only the total biomass was significantly low. Presumably this means that an unidentified methodological error caused zooplankton to be under-sampled in Petit Renaud.

Variable	t statistic	P
log ZB	3.92	0.001
log CRB	3.75	0.001
log CLB	3.72	0.001

RESULTS

A wide range of trophic conditions were represented by the 29 study sites (Table 1). The total phosphorus concentrations ranged from 5.5 to 27 µg litre^{-1} and chlorophyll *a* ranged from 1.3 to 14.2 µg litre $^{-1}$. A range in morphometric and physico-chemical variables was also observed in these dimictic temperate zone lakes (Table 2a). Most were thermally stratified in the summer.

Piscivorous fish were present in 19 of the lakes sampled and absent in the remaining 10 lakes (Table 1). Pelagic (defined here as being in water deeper than 5 m) piscivorous fish included northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*) and walleye (*Stizostedion vitrieum*). Yellow perch (*Perca flavescens*) is both planktivorous and piscivorous at different stages in its lifecycle. Any *P. flavescens* greater than 100 mm in length was considered to be piscivorous.

The effects of trophic status and piscivorous fish on the biomass and community structure of phytoplankton and zooplankton were examined as described above. These relationships will be examined in the following sections under the sub-headings of Bottom-Up, Top-Down, and the interaction between Trophic Status and Top-Down effects. A list of the variables used in this analysis is provided in Table 2b.

1. BOTTOM-UP RELATIONSHIPS

Log Chl *a* was strongly related to log TP in this data set (Table 3a & Figure 2).

$$\log \mathrm{Chl}\ a = 1.046[\log \mathrm{TP}] - 0.606$$

(r= 0.85; p= 0.001; n= 28)

The significant relationship between log Chl *a* and log TP is consistent with many other studies in the literature. For instance Dillon and Rigler (1974) found:

$$\log \mathrm{Chl}\ a = 1.449\ [\log \mathrm{TP}] - 1.136$$

(r = 0.95, p= 0.000001, n=46). Their regression is compared graphically with this study's data in Figure 3.

McCauley *et al.* (1989) and Watson *et al.* (1992) found that the log TP-log Chl *a* relationship was sigmoidal, and that a polynomial regression would better model this relationship. In our data, second and third order polynomial terms do not explain any more of the residual variability in log Chl *a* than does the linear model (Table 3b & 3c). However, both the observed range of log TP in this study and the sample size was much smaller then those in the former studies. This data set probably does not have the statistical power to detect non-linearities.

Total zooplankton biomass was not related to either total phosphorus or phytoplankton biomass; neither were any of its components (Table 3a & Figures 4-9). These results are in contrast to the results of Pace (1986) who found the following significant relationship (Figure 4):

$$[\log ZB] = 0.643\ [\log TP] + 1.582$$

(r= 0.93, p<0.0001, n= 12)

However, zooplankton community size structure is related to trophic status and phytoplankton biomass. In richer lakes, the zooplankton are generally smaller (Table 3a & Figures 10-11):

$$MDW = -0.610\ [\log TP] + 0.050$$

(r= -0.578; p= 0.001; n= 28)

$$MDW = -0.516\ [\log Chl\ a] - 0.360$$

(r= -0.604; p= 0.001; n= 28)

Zooplankton communities in richer lakes also tend to be more uniform in size as indicated by the significant negative relationship between VDW and log TP and VDW and log Chl *a* (Table 3a & Figures 12-13):

$$VDW = -0.504\ [\log TP] + 0.898$$

(r= -0.614; p= 0.001; n= 28)

$$VDW = -0.394\ [\log Chl\ a] + 0.558$$

(r= -0.593; p= 0.001; n= 28)

2. TOP-DOWN RELATIONSHIPS

Presence or absence of piscivorous fish had a significant impact on the biomass of only one subset of the zooplankton community: cladoceran biomass was significantly higher in lakes with piscivorous fish (Table 4a and Figure 14). The mean summer CLB for lakes without piscivorous fish communities is 39 μg litre^{-1} and for lakes with piscivorous fish is 82 μg litre^{-1}. Similarly, cladoceran biomass was related to piscivorous fish abundance and was found to be significant (Table 4b). These findings are consistent with the top-down prediction and observations of other studies (Carpenter *et al.*, 1985; McQueen *et al.*, 1986).

Individual zooplankton body mass is also more variable in lakes with piscivorous fish than in those lakes without (Table 4a and Figure 14). The variance in individual zooplankton dry weight is significantly related to the index of piscivorous fish abundance (Table 4b).

Presence or absence of piscivorous fish had no significant impact on phytoplankton biomass. The one-way ANOVA demonstrates that log Chl *a* did not differ significantly between lakes with and without piscivorous fish (Table 4a and Figure 15). The Spearman rank correlation using the index of piscivorous fish abundance (log PFA) leads to the same conclusion (Table 4b) . This finding is not consistent with the cascading trophic interaction hypothesis, which predicts that lower chlorophyll *a* concentrations would be expected in lakes with piscivorous fish.

Although differences in the zooplankton size structure were related to piscivorous fish presence, the variation in the algal size structure was not. Log Chl *a* did not differ for any one of the four size classes in lakes with or without piscivorous fish (Table 4c & Figure 15). The same result is tested by the interaction term between size class and fish presence or absence indicating that there is no detectable effect of piscivorous fish on the size class structure of phytoplankton.

To determine whether zooplankton biomass and size structure explain any residual variability in the log TP-log Chl *a*, relationship the partial correlations between log Chl *a* and log ZB, log CRB, log CLB, MDW and VDW were tested, while controlling for log TP. Log ZB, log CRB and log CLB all explain a significant fraction of the residual variability in the log TP-log Chl *a* relationship (Table 5 and Figures 16-20). These three variables explained 24, 18 and 22 % of the residual variability in phytoplankton biomass, respectively. Each of the variables were then combined each in turn with log TP (as independent variables) in three multiple regression models (Table 6), the resulting model statements are:

$$\log \mathrm{Chl}\ a = 1.051[\log \mathrm{TP}] - 0.280[\log \mathrm{ZB}] + 0.004$$

(r= 0.89, p= 0.001, n= 28)

$$\log \text{Chl } a = 1.015[\log \text{TP}] - 0.211[\log \text{CRB}] - 0.129$$

(r= 0.88, p= 0.001, n= 28)

$$\log \text{Chl } a = 1.012[\log \text{TP}] - 0.131[\log \text{CLB}] - 0.355$$

(r= 0.88, p= 0.001, n= 28)

In these models the additional terms improve r over the simple log TP-log Chl *a* relationship by 0.05, 0.04 and 0.04 respectively. In other words, they explain 1.2, 1.1 and 1.1 % of the residual variability.

In contrast, the indices of zooplankton community size structure had no detectable effect on the residual variability of the log TP-log Chl *a* relationship (Table 5).

Finally, it is important to note that the inclusion of the outlier point (Petit Renaud) has a significant impact on these results in particular. If the outlier point is included, all of the correlations involving the zooplankton variables (biomass or size structure) become non-significant. The impact of the inclusion of Petit Renaud on the other relationships discussed above is less marked. The only other conclusion which would differ is the effect of PFISH on log CRB, which becomes significant if the outlier point is included in the data set. However, the residuals then become strongly non-normal, due to the strong influence of Petit Renaud.

3. TROPHIC STATUS AND TOP DOWN EFFECTS

McQueen *et al.* (1986) hypothesized that in eutrophic lakes top-down effects were weaker than in oligotrophic lakes. This hypothesis was tested by examining the effect of the interaction of PFISH and log TP on log Chl *a* and log ZB, log CRB, log CLB, MDW and VDW respectively using an ANCOVA (Table 7).

The interaction term between trophic status and fish presence or absence (log TP*PFISH) had no significant effect on any of the dependent variables. Thus, there is no evidence that the strength of top-down effects depends on the trophic richness of a lake.

Table 1- List of 29 sample lakes including their location, total phosphorus concentration (μg litre^{-1}) and presence (1) or absence (0) of piscivorous fish. Sites are listed in order of increasing total phosphorus concentration. The Laurentian lakes are near St-Hippolyte, north of Montréal, Québec. The Rideau lakes are near Kingston, Ontario, and the Gatineau lakes are in Gatineau Park, Québec, north of Ottawa, Ontario.

LAKE	LOCATION	TOTAL PHOSPHORUS	PFISH
Croche	Laurentians	5.9	1
Gould	Rideau	6.8	1
Kidder	Gatineau	5.5	0
Le Blanc	Gatineau	6.5	1
Meech	Gatineau	6.0	1
Harrington	Gatineau	7.4	1
Taylor	Gatineau	8.8	1
Kingsmere	Gatineau	9.8	0
Philippe	Gatineau	9.8	1
La Pêche	Gatineau	9.8	1
Triton	Laurentians	10.1	0
Geai	Laurentians	10.2	0
Pin Rouge	Laurentians	11.4	1
Cromwell	Laurentians	13.4	1
Ramsey	Gatineau	13.5	0
Black	Gatineau	14.0	0
Petit Renaud	Gatineau	15.6	0
Upper Beverley	Rideau	15.7	1
Loutre	Gatineau	16.2	1
Sydenham	Rideau	16.2	1
Big Rideau	Rideau	16.3	1
Vase	Gatineau	16.7	0
Mulvihill	Gatineau	20.1	0
Opinicon	Rideau	22.1	1
Lower Beverley	Rideau	22.9	1
Renaud	Gatineau	23.7	1
Brown	Gatineau	24.9	1
Carmen	Gatineau	27.0	1

***For latitude and longitude coordinates refer to Appendix A.

Table 2a- The range of morphometric and physico-chemical variables encountered in the 29 lakes sampled.

Factor	Range
Temperature, Celcius	19.5 - 24.1
Conductivity, μmhos cm^{-2}	18.2 - 273
Alkalinity, μeq litre^{-1}	20.1 - 2560
pH	6.0 - 8.8
Secchi, m	1.3 - 7.5
Surface Area, ha	1.3 - 4700
Mean Depth, m	0.6 - 21.9
Maximum Depth, m	1.8 - 95

Table 2b- Description and range of untransformed limnological variables measured in the 29 study lakes.

VARIABLE	MINIMUM	MAXIMUM	REMARKS
Total Phosphorus	5.52 (μg·L^{-1})	27.0	Measure of trophic status
Phytoplankton Biomass	1.33 (μg·L^{-1})	14.2	Phytoplankton biomass as measured by Chl *a* concentration
Zooplankton Biomass	5.77 (μg dry weight· L^{-1})	408	
Crustacean Biomass	36.8 (μg dry weight· L^{-1})	334	
Cladoceran Biomass	0.211 (μg dry weight· L^{-1})	238	
Mean Individual Zooplankton Dry Weight	-0.975	-0.077	Index of community size structure which denotes mean individual body size of the zooplankton
Variance of Individual Zooplankton Dry Weight	0.086	0.76	Index of community size structure which denotes the variance in the individual body size of the zooplankton.
Piscvorous Fish Abundance	16	598	Index of piscivorous fish abundance (catch/48 hour period).
Piscivorous Fish Presence or Absence	0	1	1 denotes presence and 0 denotes absence of piscivorous fish

Table 3a: Bottom Up Relationships: Summary of simple linear regression statistics for log chlorophyll *a* concentration (μg litre^{-1}) (log Chl *a*), log zooplankton biomass (μg litre^{-1}) (log ZB), log crustacean biomass (log CRB), log cladoceran biomass (log CLB), mean individual zooplankton dry weight (MDW) and variance of individual zooplankton dry weight (VDW) using log total phosphorus concentration (log TP) and log chlorophyll *a* concentration (log Chl *a*) as an independent variable.

Indep Var	Dep Var	n	r	P
log TP	log Chl *a*	28	0.85	0.001
log TP	log ZB	28	0.02	n.s.
log TP	log CRB	28	-0.11	n.s
log TP	log CLB	28	-0.11	n.s.
log TP	MDW	28	-0.58	0.001
log TP	VDW	28	-0.61	0.001
log Chl *a*	log ZB	28	-0.25	n.s.
log Chl *a*	log CRB	28	-0.32	n.s
log Chl *a*	log CLB	28	-0.34	n.s
log Chl *a*	MDW	28	-0.60	0.001
log Chl *a*	VDW	28	-0.59	0.001

n.s $p>0.08$

Table 3b- Summary of second order polynomial regression examining the effect of log total phosphorus concentration (log TP) and log total phosphorus^2 (log TP^2) on log chlorophyll *a* concentration (log Chl *a*) for 28 lakes.

Dependent variable: log Chl *a*

SOURCE	COEFFICIENT	STD ERR	STD COEF	P
log TP	1.49	1.47	1.21	0.32
log TP^2	-0.21	0.68	-0.36	0.76

Table 3c- Summary of third order polynomial regression examining the effect of log total phosphorus concentration (log TP), log total phosphorus^2 (log TP^2) and log total phosphorus^3 (log TP^3) on log chlorophyll *a* concentration (log Chl *a*) for 28 lakes.

SOURCE	COEFFICIENT	STD ERR	STD COEF	P
log TP	0.92	14.1	0.74	0.95
log TP^2	0.34	13.2	0.59	0.98
log TP^3	-0.17	4.03	-0.49	0.97

Table 4a: Top-Down Relationships: Summary of results of One-Way ANOVA models for log chlorophyll *a* concentration (log Chl *a*), log zooplankton biomass (log ZB), log crustacean biomass (log CRB), log cladoceran biomass (log CLB), mean individual zooplankton dry weight (MDW) and variance of individual zooplankton dry weight (VDW) using piscivorous fish presence or absence (PFISH) as an independent variable.

Indep Var	Dep Var	n	F	P
PFISH	log Chl *a*	28	0.03	n.s.
PFISH	log ZB	28	0.73	n.s.
PFISH	log CRB	28	2.48	n.s.
PFISH	log CLB	28	4.79	0.04
PFISH	MDW	28	2.22	n.s.
PFISH	VDW	28	4.55	0.04

n.s. p>0.13

Table 4b- Summary of Spearman rank correlations between the log piscivorous fish abundance index (log PFA) and a) log chlorophyll *a* concentration (log Chl *a*), b) log zooplankton biomass (log ZB), c) log crustacean biomass (log CRB), d) log cladoceran biomass (log CLB), e) mean (MDW) and f) variance in individual zooplankton dry weight (VDW) for 18 lakes.

Var	n	r	P
log Chl *a*	18	-0.21	n.s.
log ZB	18	0.09	n.s.
log CRB	18	0.23	n.s.
log CLB	18	0.55	0.02
MDW	18	0.33	n.s.
VDW	18	0.47	0.05

n.s. p>0.18

Table 4c- Summary of an analysis of covariance model for log chlorophyll *a* concentration (μg litre^{-1}) (log Chl *a*) using piscivorous fish presence or absence (PFISH), size class (SIZE) and the interaction term as the independent variables. For this analysis n= 116.

Dependent variable: log Chl *a*

SOURCE	SS	DF	MS	F-RATIO	P
PFISH	0.04	1	0.04	0.29	0.59
SIZE[a]	5.69	3	1.90	14.2	0.0001
PFISH*SIZE	0.37	3	0.12	0.92	0.44
ERROR	13.9	104	0.13		

[a]Size was denoted by 1-4. (Pico=1; Nano=2; Micro=3; Net=4)

Table 5- A summary of partial correlations, after controlling for log total phosphorus (log TP), between log chlorophyll *a* concentration (log Chl *a*), log zooplankton biomass (log ZB), log crustacean biomass (log CRB), and log cladoceran biomass (log CLB) and the two indices of zooplankton community size structure (MDW & VDW).

Indep Var	n	partial r	P
log ZB	28	-0.49	0.01
log CRB	28	-0.42	0.03
log CLB	28	-0.47	0.01
MDW	28	-0.26	n.s.
VDW	28	-0.17	n.s.

n.s. p>0.17

Table 6- Summary of three multiple regressions examining the effect of log total phosphorus concentration (log TP) and a) log zooplankton biomass (log ZB) b) log crustacean biomass (log CRB) and c) log cladoceran biomass (log CLB) on chlorophyll *a* concentration (log Chl *a*) for 28 lakes.

A. Dependent variable: log Chl *a* r^2= 0.79

SOURCE	COEFFICIENT	STD ERR	STD COEF	P
CONSTANT	0.004	0.25	0.000	0.99
log TP	1.05	0.12	0.85	0.00
log ZB	-0.28	0.01	-0.26	0.01
SOURCE	**SS**	**DF**	**F-RATIO**	**P**
REGRESSION	1.37	2	45.6	0.00
RESIDUAL	0.38	25		

B. Dependent variable: log Chl *a* r^2= 0.77

SOURCE	COEFFICIENT	STD ERR	STD COEF	P
CONSTANT	-0.13	0.24	0.00	0.60
log TP	1.02	0.12	0.82	0.00
log CRB	-0.21	0.09	-0.23	0.03
SOURCE	**SS**	**DF**	**F-RATIO**	**P**
REGRESSION	1.34	2	41.2	0.00
RESIDUAL	0.41	25		

C. Dependent variable: log Chl *a* r^2= 0.78

SOURCE	COEFFICIENT	STD ERR	STD COEF	P
CONSTANT	-0.36	0.16	0.00	0.04
log TP	1.01	0.12	0.82	0.00
log CLB	-0.13	0.05	-0.25	0.01
SOURCE	**SS**	**DF**	**F-RATIO**	**P**
REGRESSION	1.36	2	44.0	0.00
RESIDUAL	0.39	25		

Table 7- Summary of ANCOVA's examining the effect of log total phosphorus concentration (log TP) and the presence or absence of piscivorous fish (FISH) on a) log chlorophyll *a* concentration (log Chl *a*), b) log zooplankton biomass (log ZB), c) log crustacean biomass (log CRB), d) log cladoceran biomass (log CLB), e) mean (MDW) and f) variance in individual zooplankton dry weight (VDW) for 29 lakes.

A. Dependent variable: log Chl *a*

Source	SS	DF	F-Ratio	P
PFISH	0.004	1	0.19	0.67
log TP	0.86	1	42.1	0.000
log TP*PFISH	0.004	1	0.21	0.66
ERROR	0.49	24		

B. Dependent variable: log ZB

Source	SS	DF	F-Ratio	P
PFISH	0.15	1	2.66	0.12
log TP	0.05	1	0.92	0.35
log TP*PFISH	0.13	1	2.29	0.14
ERROR	1.35	24		

C. Dependent variable: log CRB

Source	SS	DF	F-Ratio	P
PFISH	0.11	1	1.48	0.24
log TP	0.00	1	0.01	0.94
log TP*PFISH	0.07	1	0.97	0.33
ERROR	1.73	24		

Table 7- continued

D. Dependent variable: CLD

Source	SS	DF	F-Ratio	P
PFISH	0.42	1	2.03	0.17
log TP	0.002	1	0.01	0.92
log TP*PFISH	0.25	1	1.20	0.29
ERROR	4.98	24		

E. Dependent variable: MDW

Source	SS	DF	F-Ratio	P
PFISH	0.11	1	3.95	0.06
log TP	0.13	1	4.80	0.04
log TP*PFISH	0.08	1	2.82	0.11
ERROR	0.65	24		

E. Dependent variable: VDW

Source	SS	DF	F-Ratio	P
FISH	0.06	1	4.73	0.04
log TP	0.10	1	8.04	0.01
log TP*PFISH	0.04	1	2.88	0.10
ERROR	0.31	25		

Figure 2- The relationship between summer total chlorophyll *a* concentration (μg litre^{-1}) and summer total phosphorus concentration (μg litre^{-1}) in the 29 lakes. The solid line represents the regression model fitted to these data (model: log Chl *a* = 1.046[logTP] - 0.606). The 95 % confidence intervals are represented by the dashed lines. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

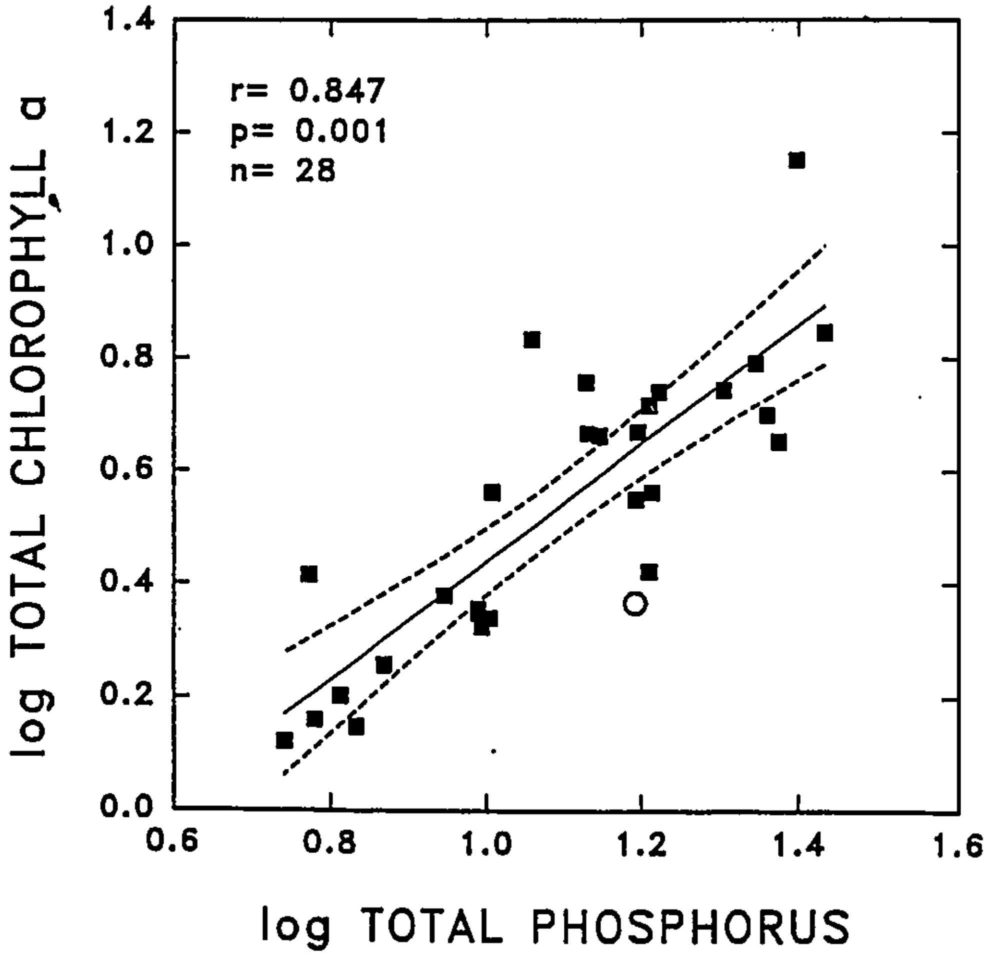

r= 0.847
p= 0.001
n= 28
log TOTAL CHLOROPHYLL a
log TOTAL PHOSPHORUS
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0.6
0.8
1.0
1.2
1.4
1.6

Figure 3- The same relationship as in Figure 2. The solid line represents this study's regression model, and the dashed line refers to the regression model of Dillon and Rigler (1974) which has been fitted for comparison. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

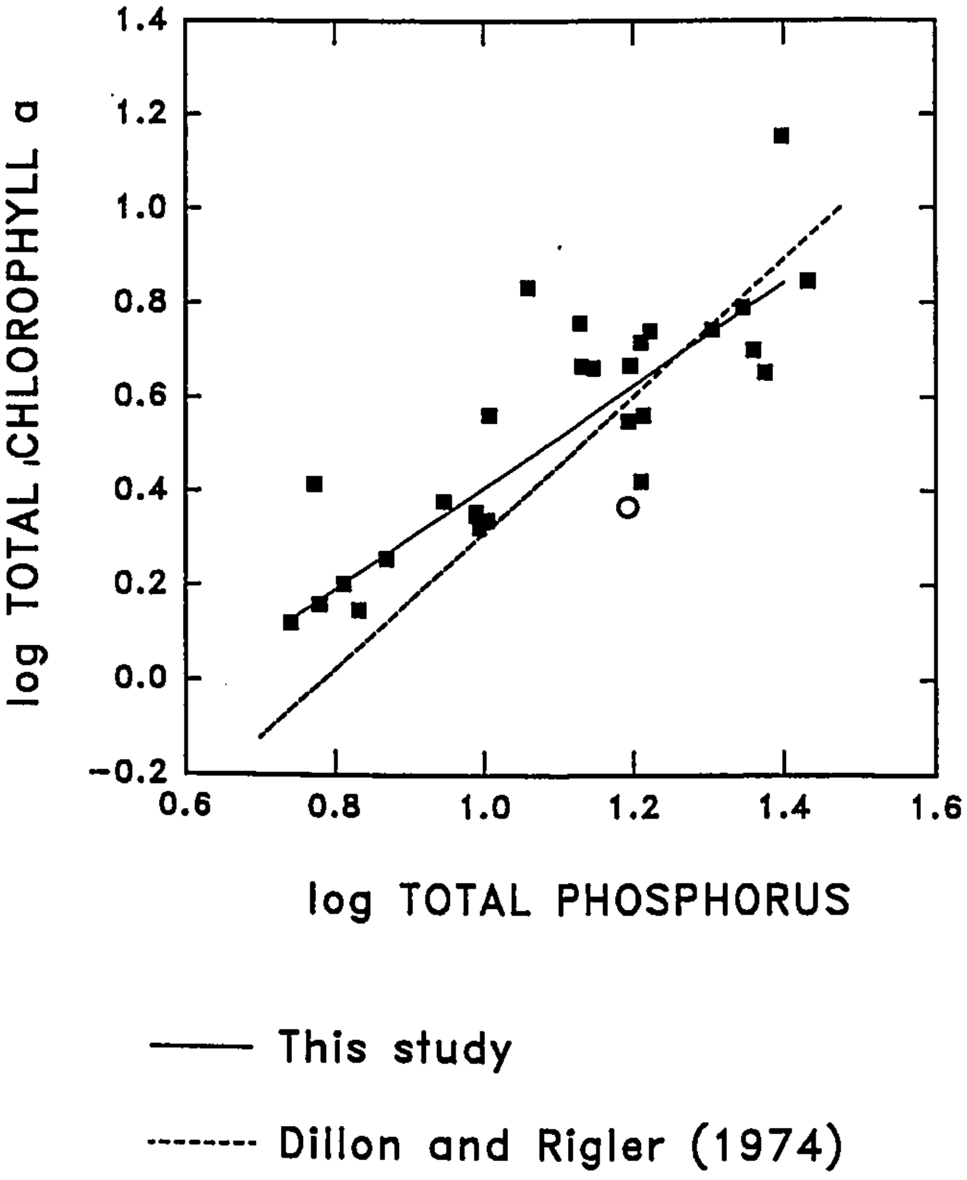
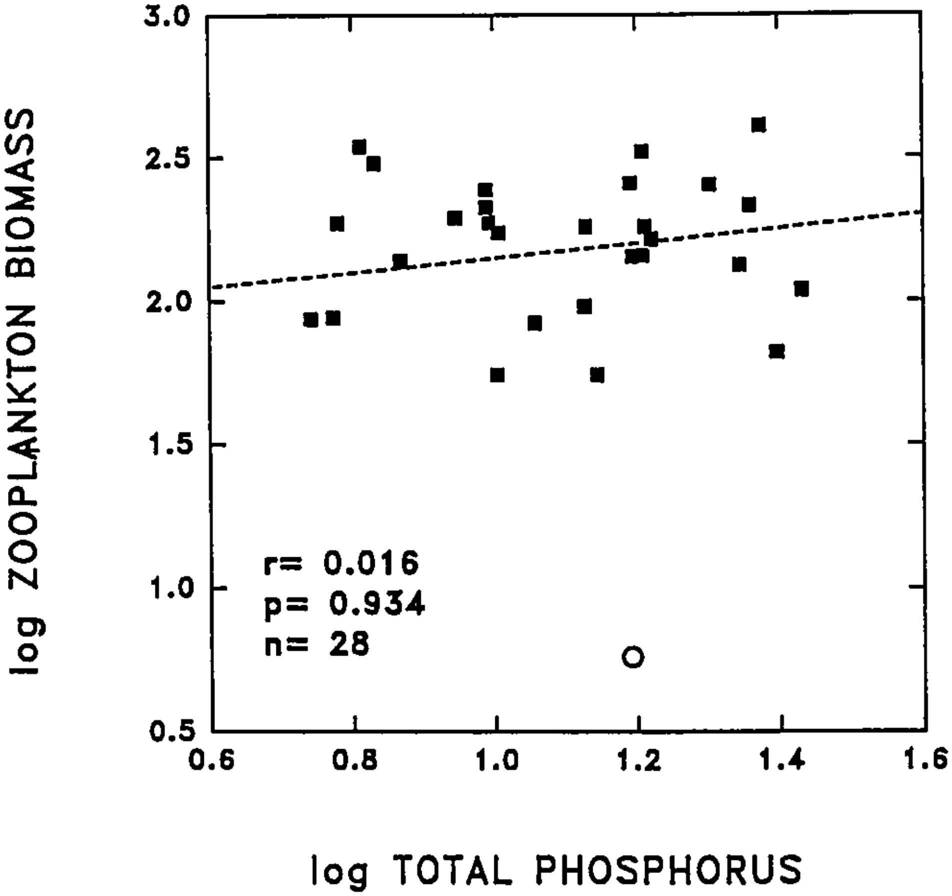

1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
−0.2
0.6
0.8
1.0
1.2
1.4
1.6
log TOTAL CHLOROPHYLL a
log TOTAL PHOSPHORUS
This study
Dillon and Rigler (1974)

Figure 4- The relationship between mean summer zooplankton biomass (µg litre^{-1} dry weight) and mean summer total phosphorus concentration (µg litre^{-1}) in the 29 lakes. Both variables have been log transformed. The dashed line refers to the regression model of Pace (1986) which has been fitted for comparison. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.


3.0
2.5
2.0
1.5
1.0
0.5
0.6
0.8
1.0
1.2
1.4
1.6
log ZOOPLANKTON BIOMASS
log TOTAL PHOSPHORUS
r= 0.016
p= 0.934
n= 28

.... Pace(1986)

Figure 5- The relationship between mean summer zooplankton biomass (μg $litre^{-1}$ dry weight) and mean summer total chlorophyll *a* concentration (μg $litre^{-1}$) in the 29 lakes. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

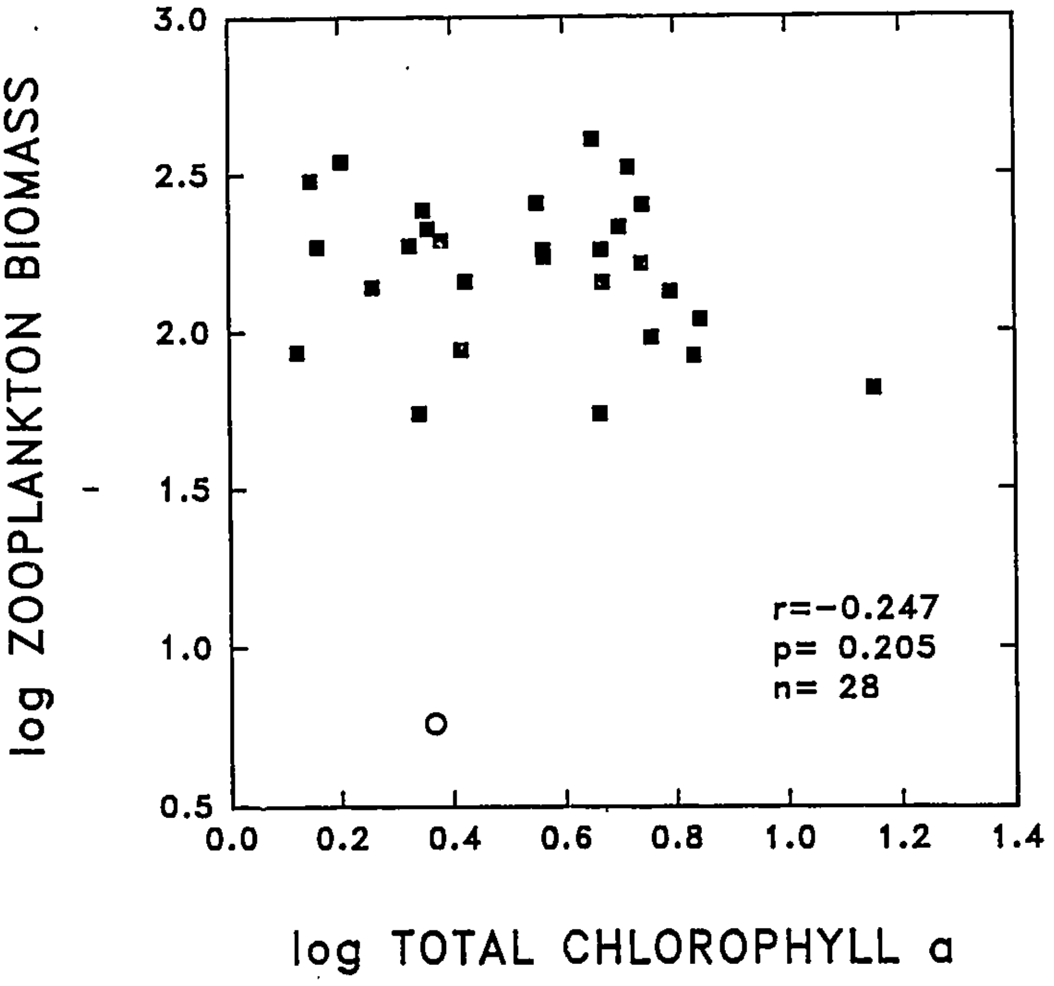

log ZOOPLANKTON BIOMASS
log TOTAL CHLOROPHYLL a
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
r=−0.247
p= 0.205
n= 28

Figure 6- The relationship between mean summer crustacean biomass (µg litre^{-1} dry weight) and mean summer total phosphorus concentration (µg litre^{-1}) in the 29 lakes. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

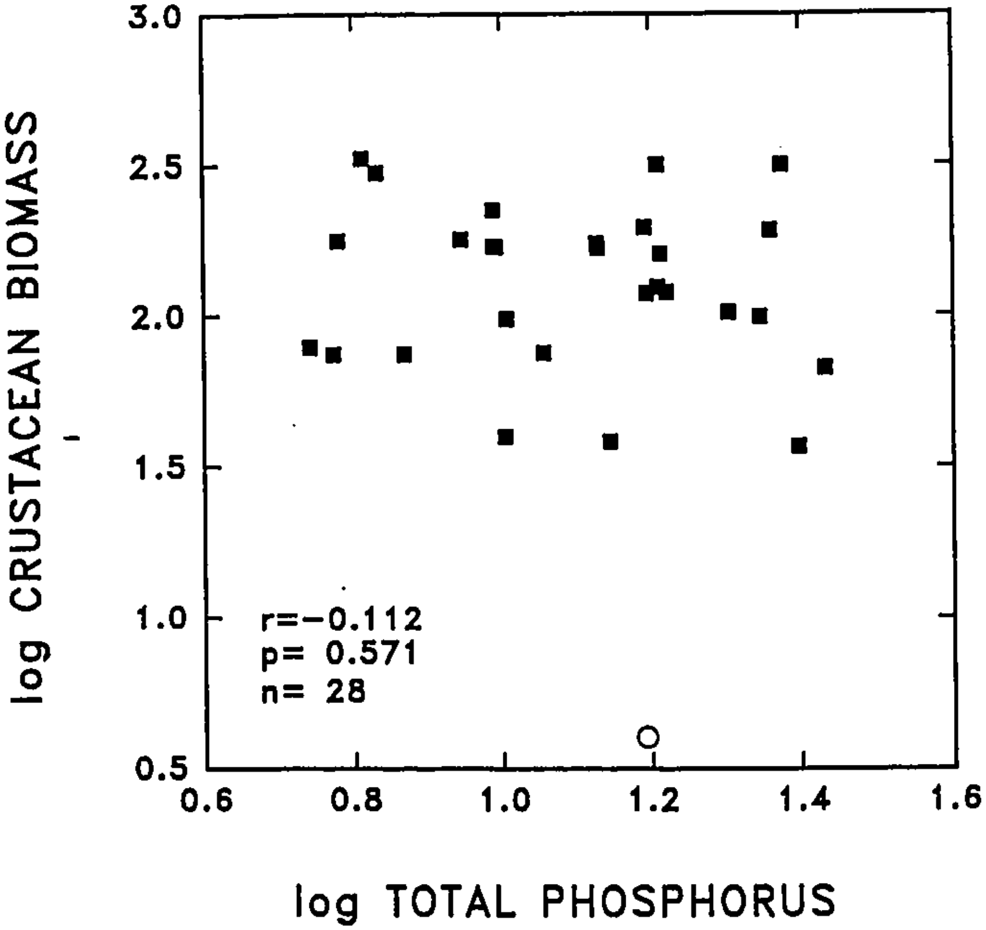

3.0
2.5
2.0
1.5
1.0
0.5
0.6
0.8
1.0
1.2
1.4
1.6
log CRUSTACEAN BIOMASS
log TOTAL PHOSPHORUS
r=−0.112
p= 0.571
n= 28

Figure 7- The relationship between mean summer crustacean biomass (µg litre^{-1} dry weight) and mean summer total chlorophyll *a* concentration (µg litre^{-1}) in the 29 lakes. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

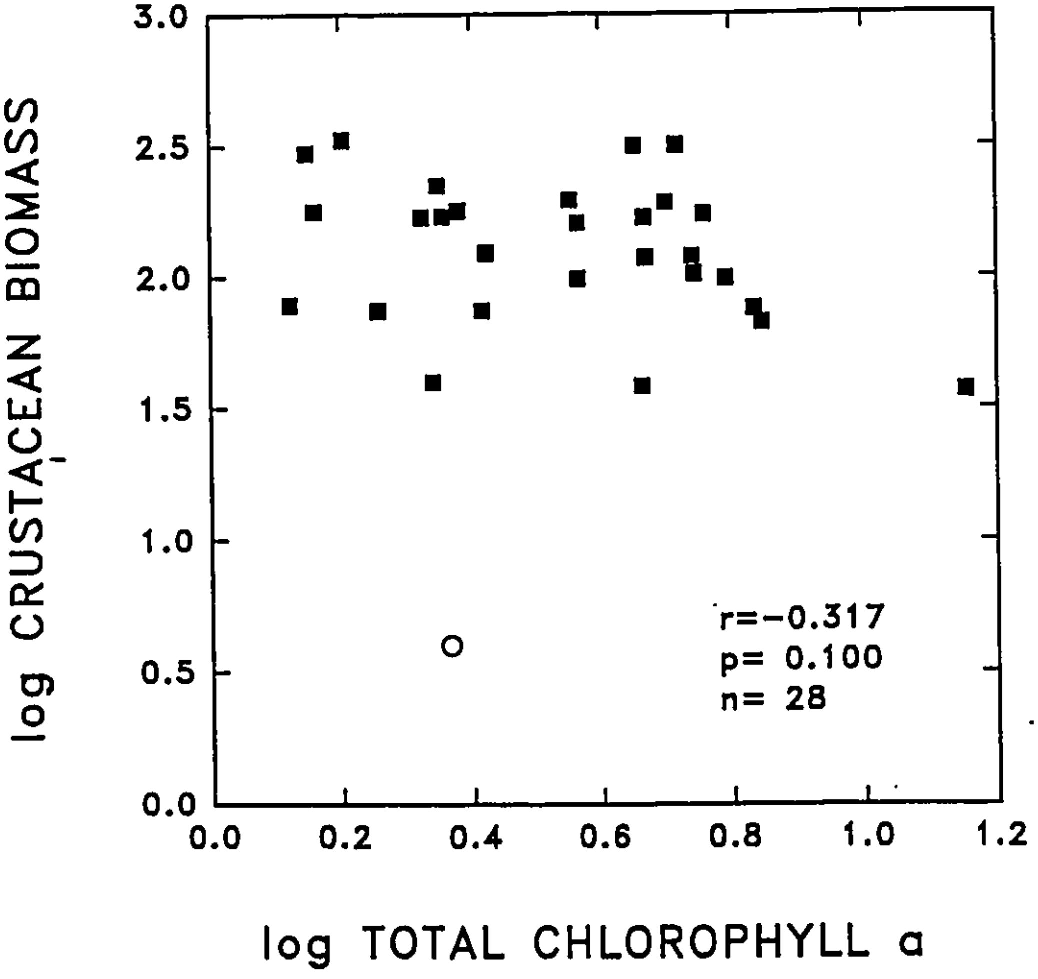

3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
log CRUSTACEAN BIOMASS
log TOTAL CHLOROPHYLL a
r=-0.317
p= 0.100
n= 28

Figure 8- The relationship between mean summer cladoceran biomass (µg litre^{-1} dry weight) and mean summer total phosphorus concentration (µg litre^{-1}) in the 29 lakes. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

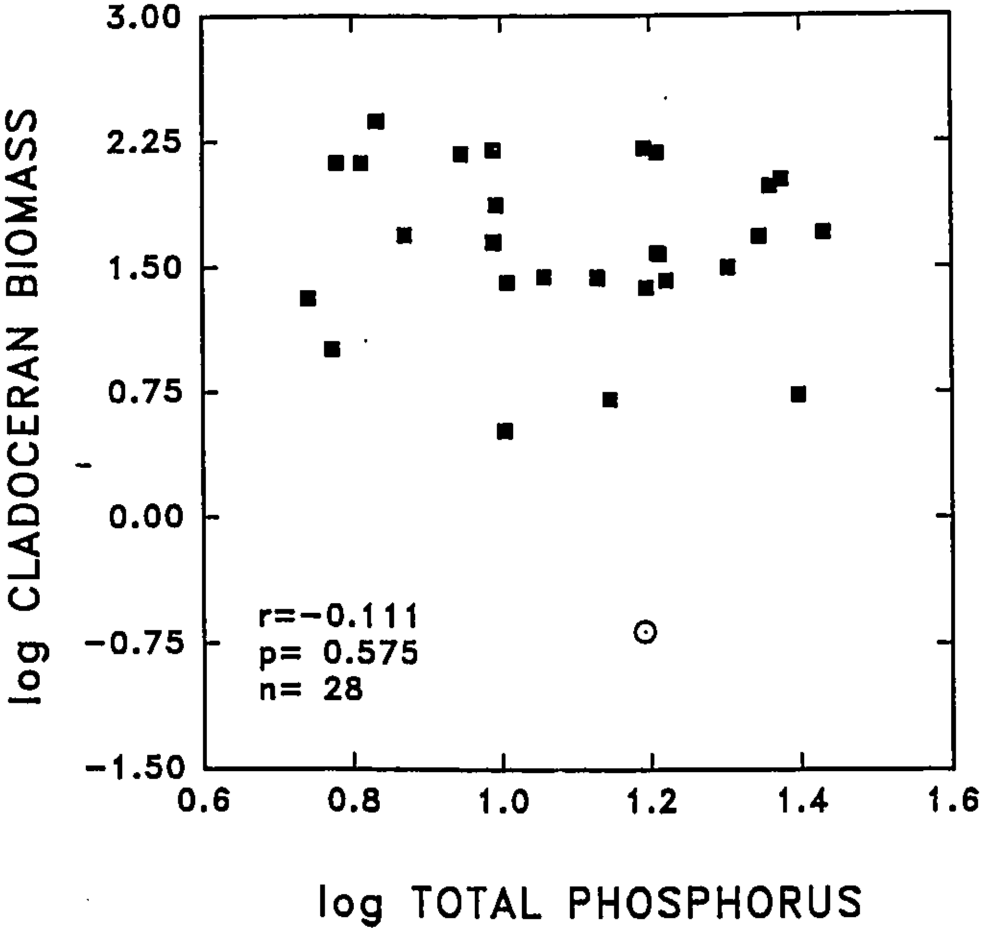

3.00
2.25
1.50
0.75
0.00
-0.75
-1.50
0.6
0.8
1.0
1.2
1.4
1.6
log CLADOCERAN BIOMASS
log TOTAL PHOSPHORUS
r=-0.111
p= 0.575
n= 28

Figure 9- The relationship between mean summer cladoceran biomass (μg litre^{-1} dry weight) and mean summer total chlorophyll *a* concentration (μg litre^{-1}) in the 29 lakes. Both variables have been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

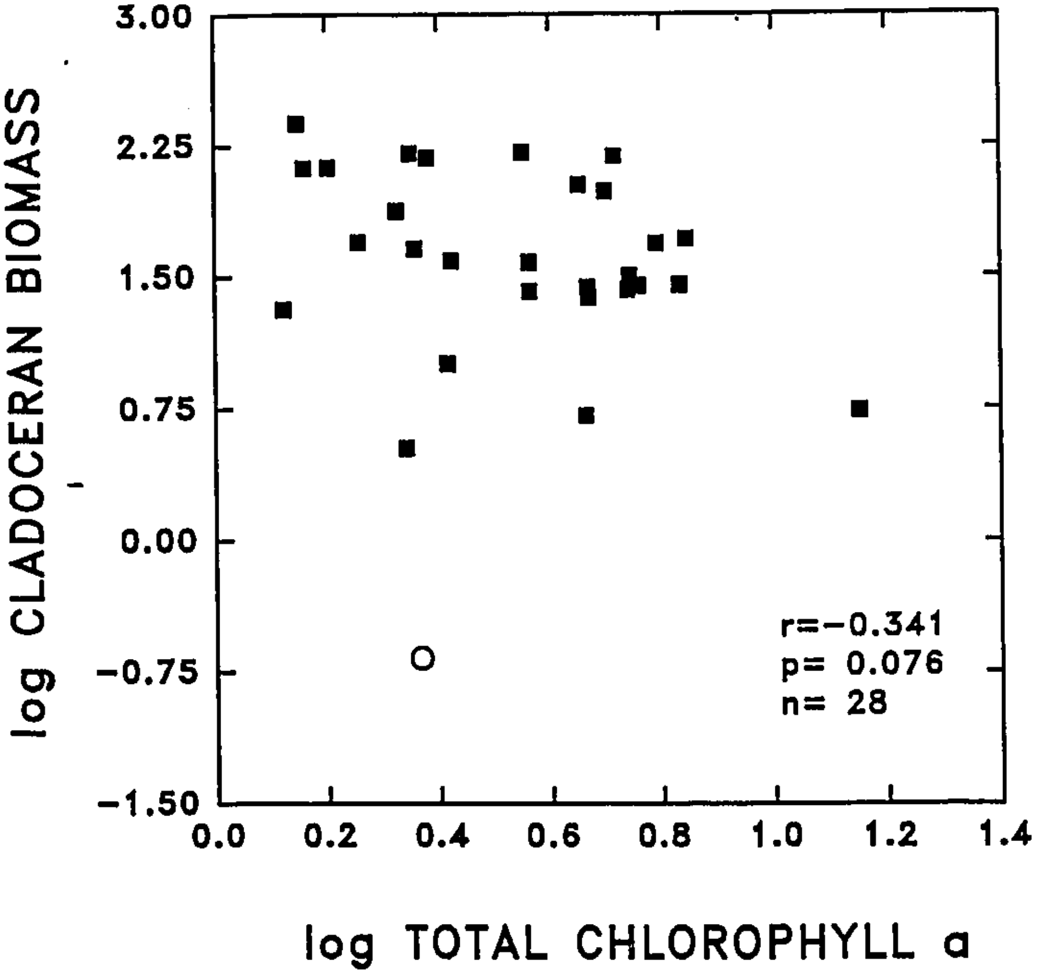

3.00
2.25
1.50
0.75
0.00
-0.75
-1.50
log CLADOCERAN BIOMASS
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
log TOTAL CHLOROPHYLL a
r=-0.341
p= 0.076
n= 28

Figure 10- The relationship between mean individual zooplankton dry weight and mean summer total phosphorus concentration (µg litre^{-1}) in the 29 lakes. The solid line represents the regression model fitted to these data. The 95 % confidence intervals are represented by the dashed lines. Total phosphorus has been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

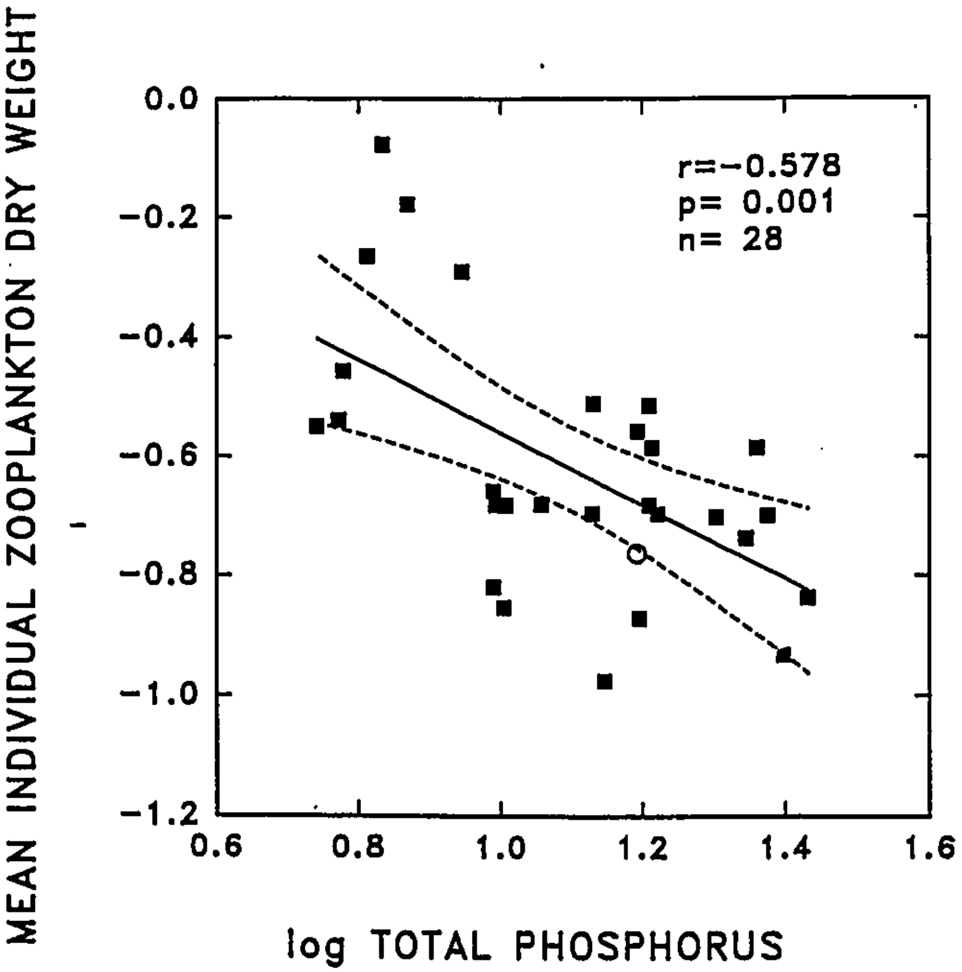

r=−0.578
p= 0.001
n= 28
MEAN INDIVIDUAL ZOOPLANKTON DRY WEIGHT
0.0
−0.2
−0.4
−0.6
−0.8
−1.0
−1.2
0.6
0.8
1.0
1.2
1.4
1.6
log TOTAL PHOSPHORUS

Figure 11- The relationship between mean individual zooplankton dry weight and mean summer total chlorophyll *a* concentration (μg $litre^{-1}$) in the 29 lakes. The solid line represents the regression model fitted to these data. The 95 % confidence intervals are represented by the dashed lines. Total chlorophyll *a* has been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

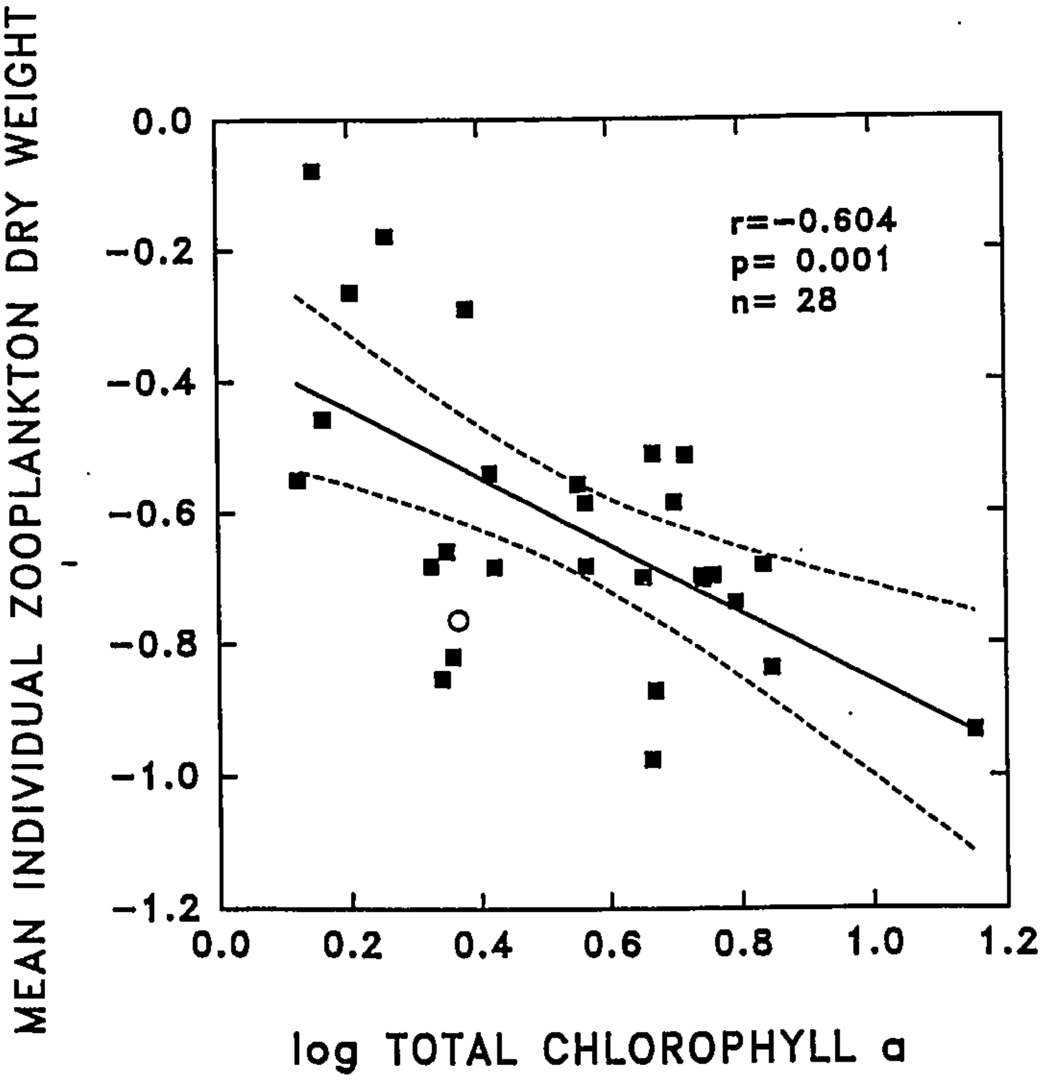

r=-0.604
p= 0.001
n= 28
MEAN INDIVIDUAL ZOOPLANKTON DRY WEIGHT
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
log TOTAL CHLOROPHYLL a

Figure 12- The relationship between variance of individual zooplankton dry weight and mean summer total phosphorus concentration (μg litre^{-1}) in the 29 lakes. The solid line represents the regression model fitted to these data. The 95 % confidence intervals are represented by the dashed lines. Total phosphorus has been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

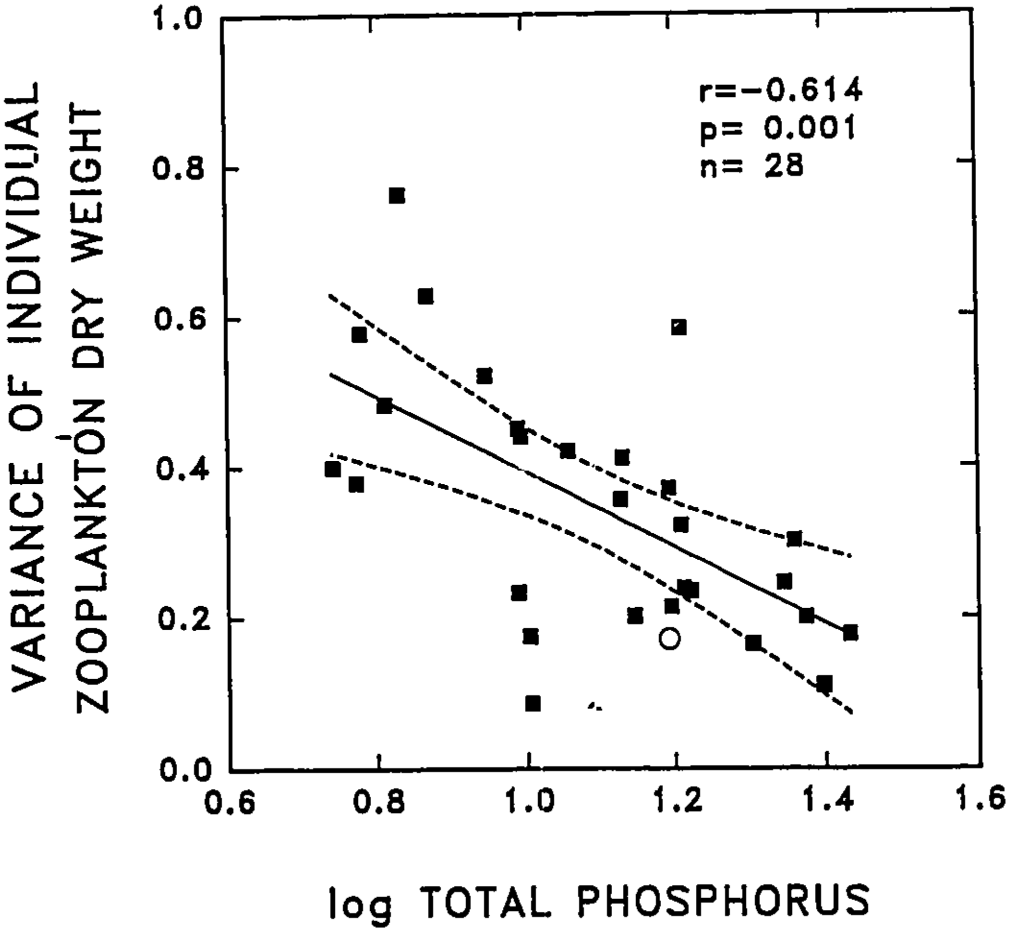

r=-0.614
p= 0.001
n= 28
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.8
1.0
1.2
1.4
1.6
VARIANCE OF INDIVIDUAL ZOOPLANKTON DRY WEIGHT
log TOTAL PHOSPHORUS

Figure 13- The relationship between variance of individual zooplankton dry weight and mean summer total chlorophyll *a* concentration (µg litre^{-1}) in the 29 lakes. The solid line represents the regression model fitted to these data. The 95 % confidence intervals are represented by the dashed lines. Total chlorophyll *a* has been log transformed. The open circle in this figure represents the data for Petit Renaud, which was not used in the statistical analysis, but provided for comparison.

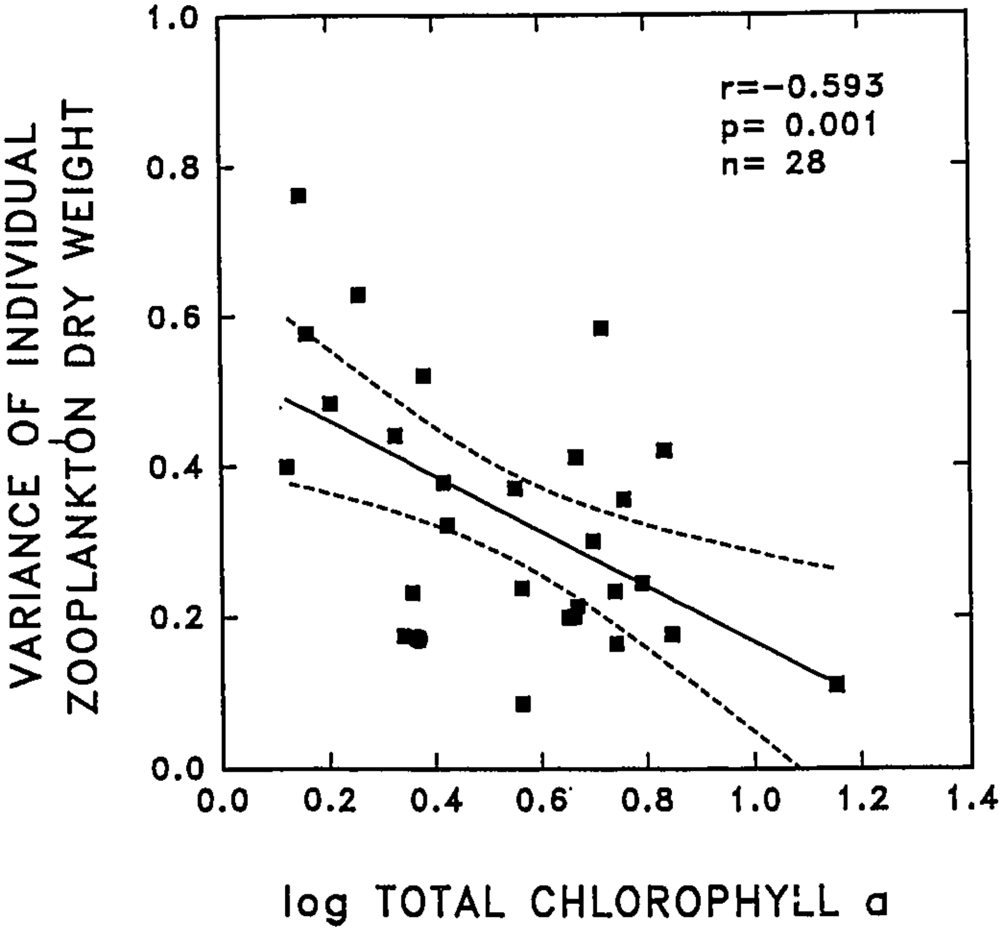

r=-0.593
p= 0.001
n= 28
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
VARIANCE OF INDIVIDUAL ZOOPLANKTON DRY WEIGHT
log TOTAL CHLOROPHYLL a

Figure 14- The effect of piscivorous fish presence or absence on zooplankton biomass and size structure of the 29 lakes. CLB represents mean summer cladoceran biomass (μg litre^{-1} dry weight), CRB represents mean summer crustacean biomass, ZB represents mean summer zooplankton biomass, MDW represents mean individual zooplankton dry weight (index of size structure) and VDW represents variance in individual zooplankton dry weight (index of size structure). The open bar represents the 10 lakes without piscivorous fish and the hatched bar represents the 19 lakes with piscivorous fish. Standard error bars are presented. ** refer to those variables which differ significantly between lakes with and without piscivorous fish (P<0.05). CLB, CRB, ZB have been log transformed.

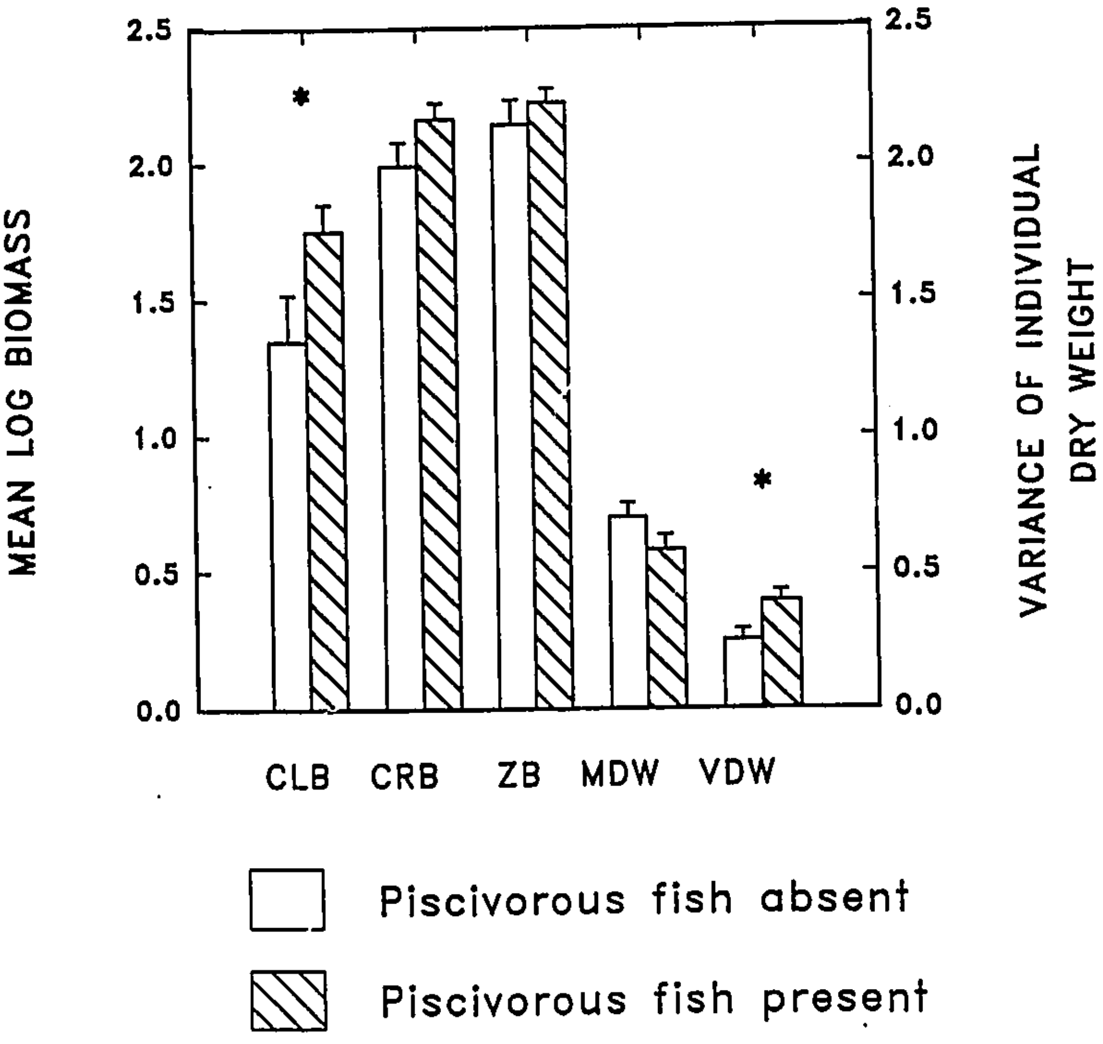

2.5
2.0
1.5
1.0
0.5
0.0
MEAN LOG BIOMASS
VARIANCE OF INDIVIDUAL DRY WEIGHT
*
*
CLB
CRB
ZB
MDW
VDW
Piscivorous fish absent
Piscivorous fish present

Figure 15- The effect of piscivorous fish presence or absence on phytoplankton biomass and size structure of the 29 lakes. All chlorophyll measurements are mean summer concentrations, the size classes are defined as: Pic<0.2 µm, 0.2<Nan<12 µm, 12<Mic<35 µm, Net>35 µm; Chl represents total chlorophyll *a* concentration. The open bar represents the 10 lakes without pisicivorous fish and the hatched bar represents the 19 lakes with piscivorous fish. Standard error bars are presented. All independent continuous variables have been log transformed.

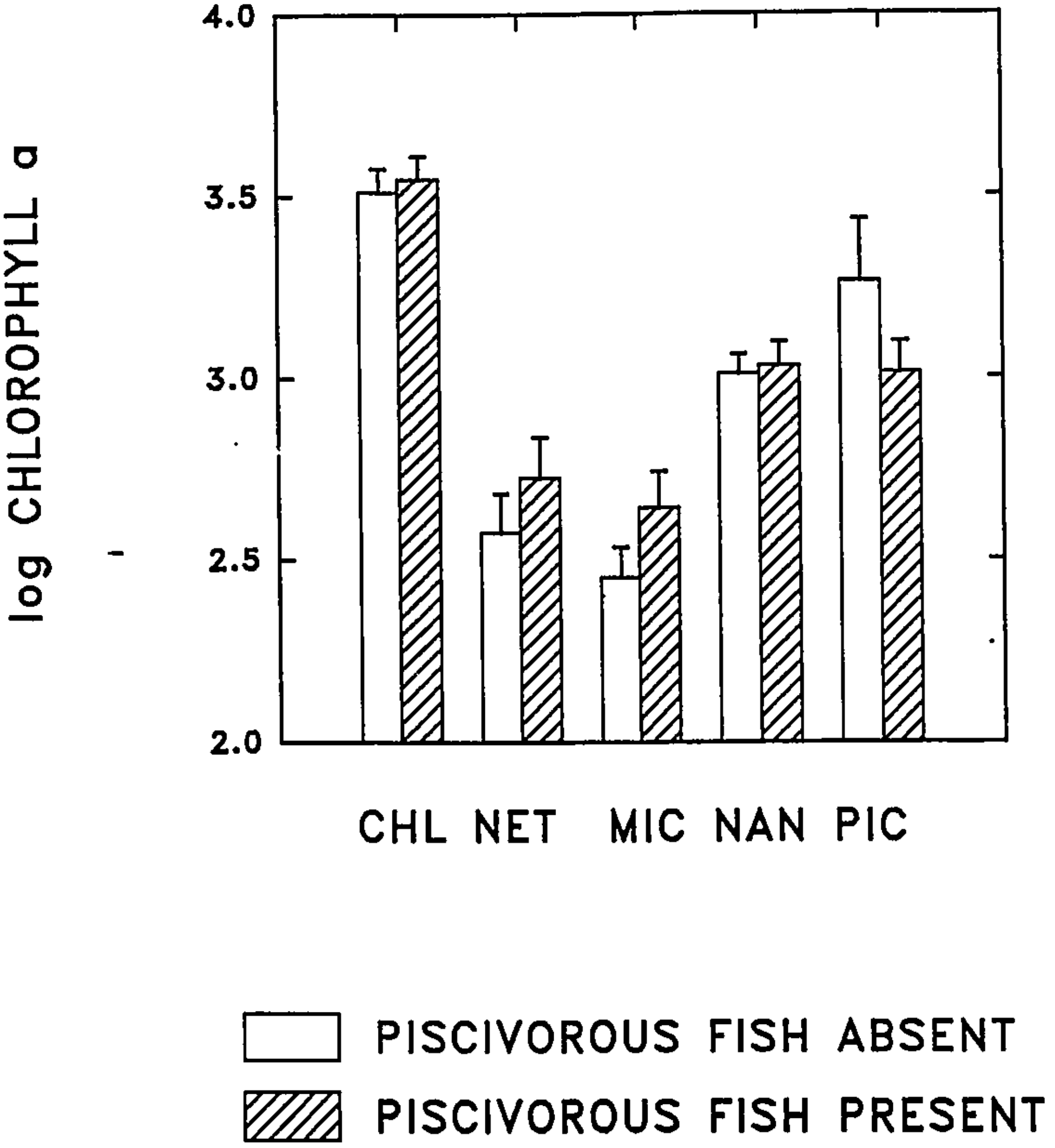

log CHLOROPHYLL a
4.0
3.5
3.0
2.5
2.0
CHL
NET
MIC
NAN
PIC
PISCIVOROUS FISH ABSENT
PISCIVOROUS FISH PRESENT

Figure 16- The relationship between the TP-Chl *a* (log total phosphorus concentration vs mean log total chlorophyll *a* concentration) residuals and the TP-ZB (log total phosphorus concentration vs log zooplankton biomass) residuals in the 28 lakes.

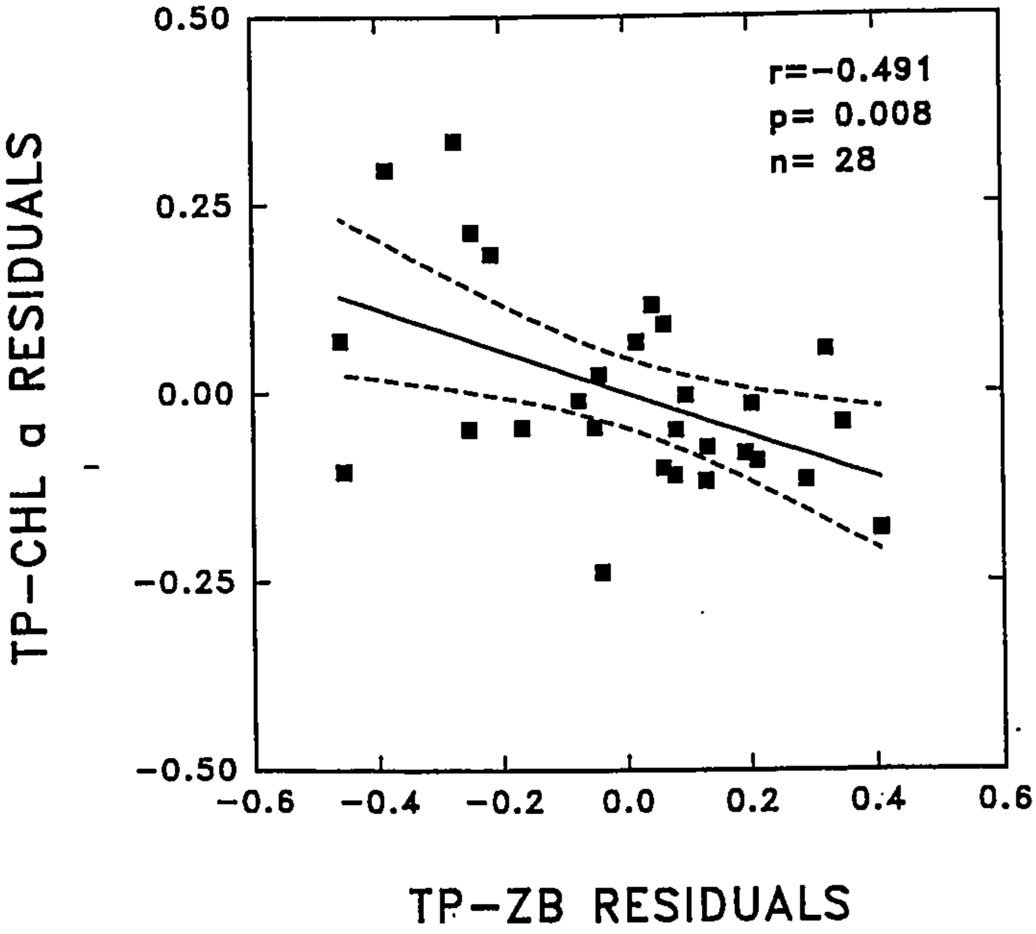

r=−0.491
p= 0.008
n= 28
0.50
0.25
0.00
−0.25
−0.50
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
TP−CHL a RESIDUALS
TP−ZB RESIDUALS

Figure 17- The relationship between the TP-Chl *a* (log total phosphorus concentration vs log total chlorophyll *a* concentration) residuals and the TP-CRB (log total phosphorus concentration vs log crustacean biomass) residuals in the 28 lakes.

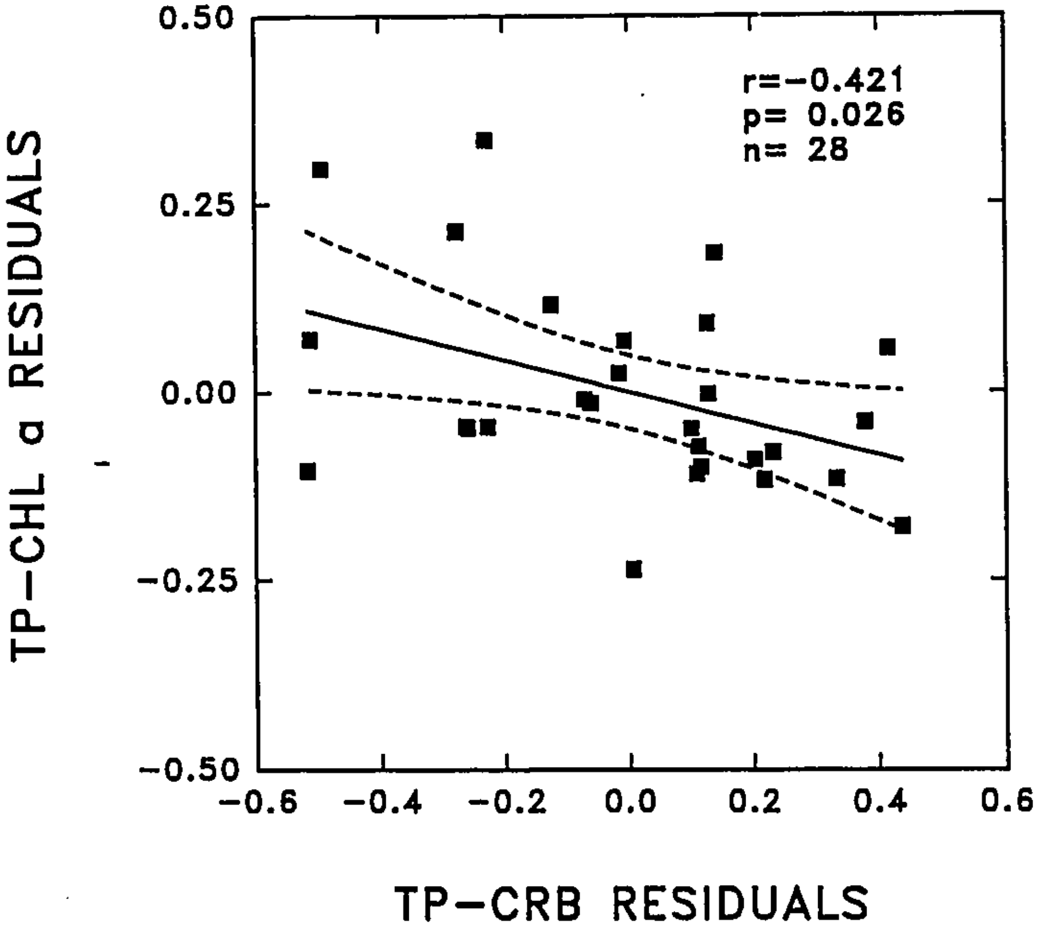

r=-0.421
p= 0.026
n= 28
0.50
0.25
0.00
-0.25
-0.50
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
TP-CHL a RESIDUALS
TP-CRB RESIDUALS

Figure 18- The relationship between the TP-Chl *a* (log total phosphorus concentration vs log total chlorophyll *a* concentration) residuals and the TP-CLB (log total phosphorus concentration vs log cladoceran biomass) residuals in the 28 lakes.

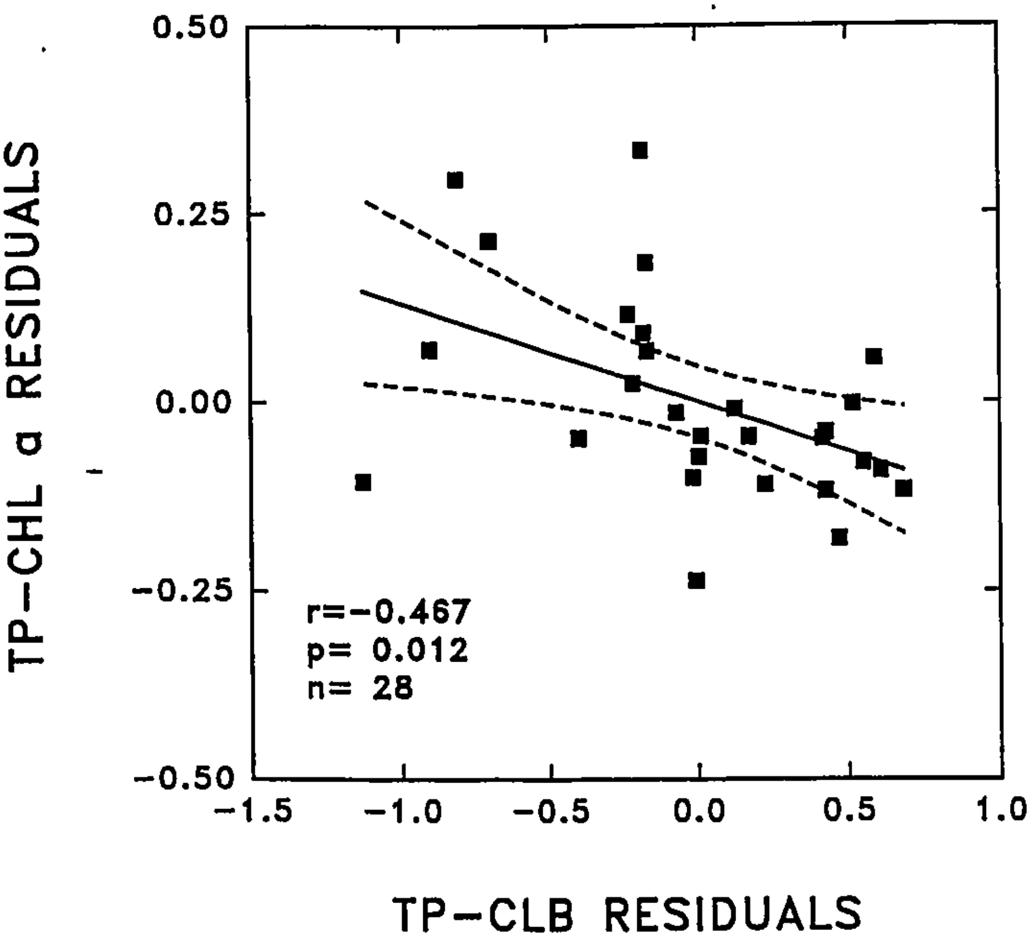

0.50
0.25
0.00
−0.25
−0.50
−1.5
−1.0
−0.5
0.0
0.5
1.0
TP−CHL a RESIDUALS
TP−CLB RESIDUALS
r=−0.467
p= 0.012
n= 28

Figure 19- The relationship between the TP-Chl *a* (log total phosphorus concentration vs log total chlorophyll *a* concentration) residuals and the TP-MDW (log total phosphorus concentration vs mean individual zooplankton dry weight) residuals in the 28 lakes.

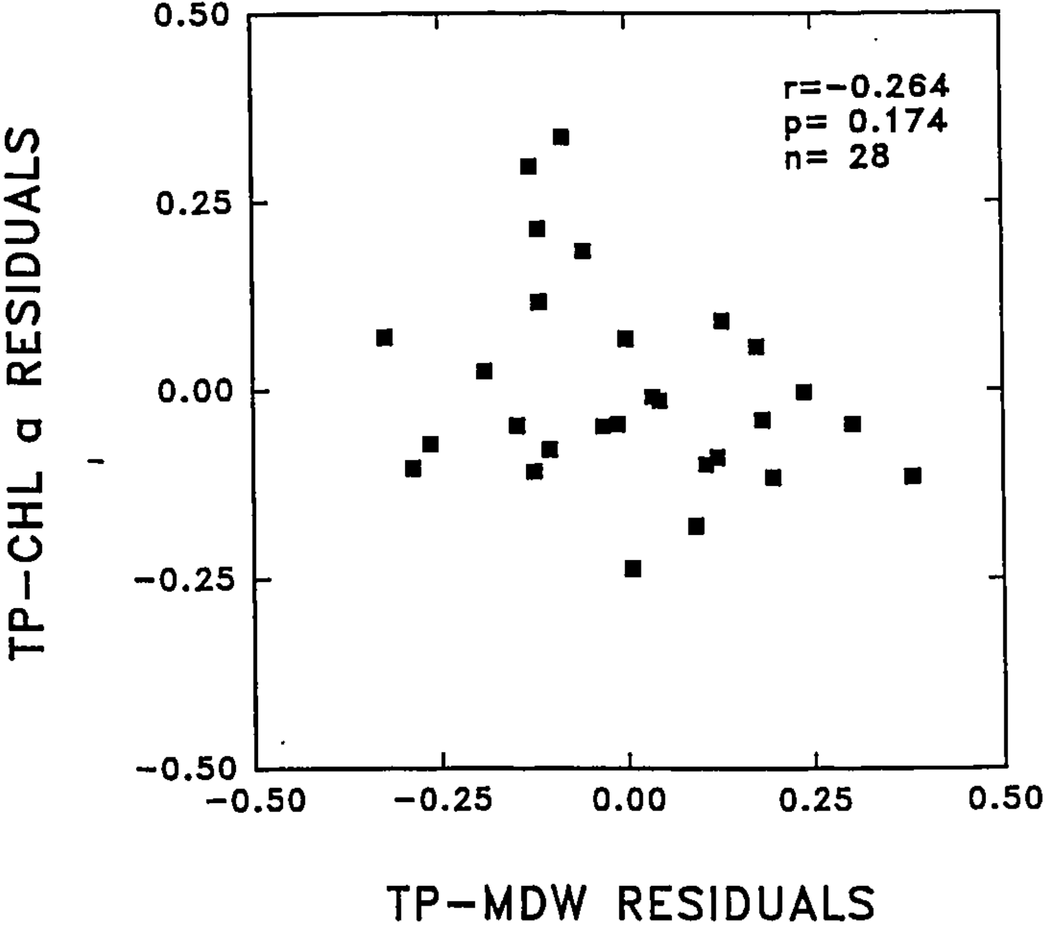
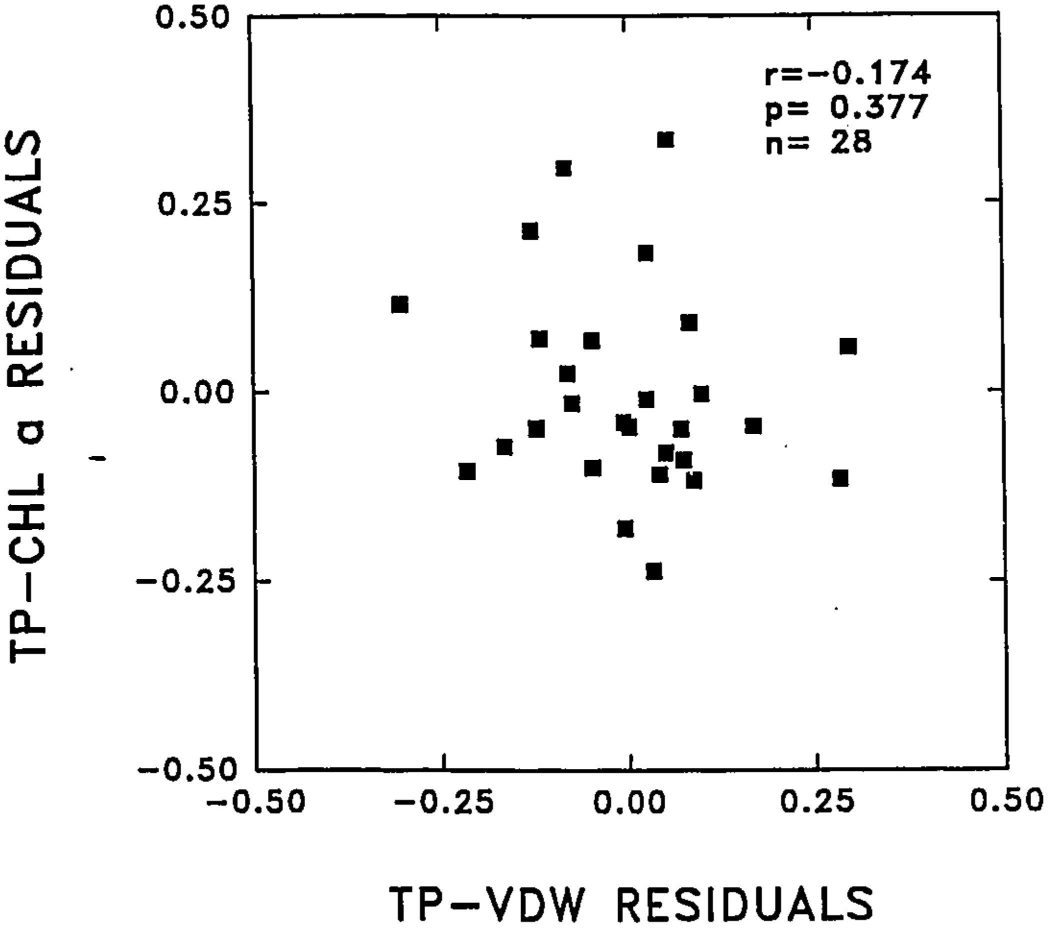

r=−0.264
p= 0.174
n= 28
0.50
0.25
0.00
−0.25
−0.50
−0.50
−0.25
0.00
0.25
0.50
TP−CHL a RESIDUALS
TP−MDW RESIDUALS

Figure 20- The relationship between the TP-Chl *a* (log total phosphorus concentration vs log total chlorophyll *a* concentration) residuals and the TP-VDW (log total phosphorus concentration vs variance in individual zooplankton dry weight) residuals in the 28 lakes.


r=−0.174
p= 0.377
n= 28
0.50
0.25
0.00
−0.25
−0.50
−0.50
−0.25
0.00
0.25
0.50
TP−CHL a RESIDUALS
TP−VDW RESIDUALS

DISCUSSION

The bottom-up hypothesis predicts that the biomass and structure of the aquatic community is ultimately controlled by nutrient availability. The bottom-up prediction most clearly supported by this study is the positive correlation between chlorophyll *a* and total phosphorus. This significant linear relationship is similar to that in many other studies (Dillon and Rigler, 1974; Janus and Vollenweider, 1981; Pace, 1984; Hanson and Peters, 1984). In fact, Figure 3 clearly demonstrates the close agreement between these results and those of Dillon and Rigler (1974).

The bottom-up predictions concerning zooplankton biomass and community size structure are less clearly supported by the results of the current study. Zooplankton biomass was not correlated with total phosphorus concentration or chlorophyll *a* concentration. While the overall biomass did not covary with lake trophic status, zooplankton community size structure was dependent on these measures of nutrient availability. In general, richer lakes have smaller zooplankton which are more uniformly distributed in size. Essentially, as the lakes increase in richness, decreases in biomass due to the loss of large zooplankton are offset by attendant increases in small zooplankton so that zooplankton biomass does not change.

A possible explanation for this relationship between zooplankton size structure and trophic status can be provided by extending the argument of

Hillbricht-Ilkowska (1977) who proposed that oligotrophic systems do not contain sufficient energy to support bacterivorous ciliates and rotifers; however, eutrophic systems have increased levels of detritus, increased bacterial activity and thus increased microzooplankton biomass and productivity. Our study examined only macrozooplankton, therefore one can extend their argument to the small macrozooplankton of this study. Bays and Crisman (1983) found that the percentage of microzooplankton relative to total zooplankton biomass increased with lake trophic state.

In contrast, in a study examining 10 Québec lakes, Pace (1986) observed that both micro- and macrozooplankton biomass increase positively with increasing total phosphorus. In his study, Pace found that zooplankton biomass, but not size structure, was related to lake richness. The converse was observed in the current study. This difference could result from at least two sources. First, our methodologies may have differed in some way that is not obvious. However, it is unlikely that these differences can be explained on the basis of sampling methodology since Pace's (1986) methods were used in this study. Further, had there been a methodological problem, it is unlikely that a relationship between zooplankton size structure and total phosphorus would have been found. Second, neither study was based upon a random sample of a defined population of lakes. As a result, the two studies may have sampled different populations.

The top-down hypothesis predicts that the biomass and structure of the aquatic community is ultimately controlled by piscivorous fish predation. In this study, top-down effects on the plankton were detectable, but weak. Piscivorous fish have an effect only on cladoceran biomass and on the variance in individual zooplankton dry weight. In accordance with the cascading trophic model, cladoceran biomass is higher in lakes with piscivorous fish present. (However, total zooplankton biomass is unaffected). As well, individual zooplankton dry weight is more variable when piscivorous fish are present. This is presumably due to the presence of large cladocerans when piscivorous fish are present. The presence of piscivorous fish results in an accompanying increase in the variance in individual zooplankton dry weight because the large cladocerans fall at the upper edge of the size distribution. The fact that total zooplankton biomass does not change implies that small zooplankton are less abundant when large cladocerans are present.

While zooplankton size and abundance were weakly related to piscivorous fish presence, algal size and abundance were not at all related to fish presence. This clearly contradicts the cascading trophic interaction hypothesis, and is of particular interest as the reduction in algal biomass is the goal of biomanipulation techniques based upon top-down manipulation (Shapiro *et al.*, 1975; Lynch and Shapiro, 1981; Shapiro and Wright, 1984).

The present results are consistent with the dampening hypothesis, which suggests that predator impacts are strongest at the top of the food chain and weaker towards the bottom (McQueen *et al.*, 1986; Lafontaine and McQueen, 1991). Our results indicate that piscivorous fish presence has a weak effect on cladoceran biomass and size, but no detectable effect on phytoplankton biomass or size structure.

Our results also support the conclusions of a recent review of top-down and biomanipulation studies by DeMelo *et al.* (1992) in which it was shown that few of the 44 food-web biomanipulations published between 1961 and 1989 actually observed a change in phytoplankton biomass or species composition. Predation effects can be masked by numerous confounding factors including algal grazability, nutrient or climatic fluctuations, direct nutrient additions by fish, dead fish effects, etc. (DeMelo *et al.* 1992). It is possible that the effects of piscivorous fish are muted or are simply not strong enough to reach this bottom level of the aquatic pelagic food web in most cases. Those studies which have observed effects of piscivorous fish on phytoplankton have in many cases have been conducted on dramatically altered lakes or enclosures. In this study we attempted to observe recently unmanipulated lake systems, and no piscivorous fish effect was evident on phytoplankton biomass or size structure. These results call into question the feasibility of biomanipulation techniques as a method of phytoplankton biomass reduction (Carpenter *et al.*, 1985; Carpenter and Kitchell, 1987; Shapiro *et al.*, 1975).

In addition to the effects of fish predation on phytoplankton biomass, some of the above studies have also examined the residual variability in chlorophyll *a*, not explained by nutrient availability. Many, including Carpenter *et al.* (1985) and Shapiro *et al.* (1975), postulate that both zooplankton biomass and size structure should explain significant portions of the residual variability. In testing this relationship, Pace (1984) and Quiros (1990) found that, while size structure indices explain a small amount of the TP-Chl *a* residual variability (a few percent), zooplankton biomass did not explain any of the residual variability.

The results of this study are the converse of those of Pace (1984) and Quiros (1990). Our indices of zooplankton community size structure did not explain a significant amount of residual variability, however zooplankton biomass did explain a significant amounts of the residual variability in the TP-Chl *a* relationship (25 %). These results are consistent with the hypothesis that biological factors other than nutrient availability are responsible for the regulation of phytoplankton biomass in natural systems. However, the results also indicate that the top-down effects are considerably weaker in comparison to nutrient control. In addition, the results demonstrate that top-down effects are significant between adjacent trophic levels, but not across more widely separated trophic levels such as piscivorous fish and phytoplankton.

There is no evidence, however, that the strength of top-down effects are mediated by trophic status as suggested by McQueen *et al.* (1986). In the present study there was no significant interaction between the presence of piscivorous fish and total phosphorus at the zooplankton or phytoplankton levels. Earlier studies that did show an interaction (e.g. Lafontaine and McQueen, 1992; Drenner, 1988) involved manipulations of two lakes or tanks, as opposed to this study which examined 29 lakes. It therefore seems reasonable to conclude that, in unmanipulated lakes, the interaction between the top-down effects of fish predation and trophic status are weak, if they exist at all.

GENERAL CONCLUSION

This study confirmed that the strongest factor determining phytoplankton biomass is nutrient availability, which alone accounts for 71 % of the among-lake variation in Chl *a*. Phytoplankton biomass is also related to measures of zooplankton biomass but its effect is much smaller, explaining only an additional 8 % of the variability in Chl *a*. Piscivorous fish have no detectable effect on chlorophyll levels.

Neither nutrient availability nor piscivorous fish presence appear to have a large effect on zooplankton. There is no measurable nutrient limitation of zooplankton biomass, and piscivorous fish presence has only a weak effect on a single component of zooplankton biomass. Zooplankton community size structure is more strongly linked to nutrient availability, with the relative amount of smaller zooplankton increasing with lake richness.

In summation, this study has demonstrated that top-down forces are relatively weak and are dampened as one proceeds down the food web. In fact, in relatively unperturbed natural systems there is little detectable effect of piscivorous fish presence on lower trophic level communities.

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APPENDIX A- Latitude and longitude coordinates for the 29 study lakes in Ontario and Québec.

LAKE	LATITUDE	LONGITUDE
Big Rideau	44°45' W	76°13'N
Black	45°30'W	75°52'N
Brown	45°36'W	75°55'N
Carmen	45°36'W	75°56'N
Croche	45°60'W	74°10'N
Cromwell	45°49'W	74°00'N
Fortune	45°31'W	75°52'N
Geai	46°00'W	74°00'N
Gould	44°28'W	76°35'N
Harrington	45°35'W	75°58'N
Kidder	45°36'W	76°06'N
Kingsmere	45°29'W	75°51'N
Lower Beverley	44°36'W	76°08'N
La Pêche	45°38'W	76°11'N
Le Blanc	45°37'W	76°08'N
Loutre	45°30'W	75°52'N
Meech	45°31'W	75°54'N
Mulvihill	45°29'W	75°51'N
Opinicon	44°34'W	76°19'N
Petit Renaud	45°36'W	76°00'N
Philippe	45°36'W	76°01'N
Pin Rouge	45°58'W	74°03'N
Ramsey	45°36'W	76°06'N
Renaud	45°36'W	76°02'N
Sydenham	44°25'W	76°33'N
Taylor	45°36'W	76°03'N
Triton	45°58'W	74°01'N
Upper Beverley	44°37'W	76°05'N
Vase	45°36'W	76°04'N

APPENDIX B-

As described in the methods section the zooplankton were counted in four distinct groups each using a different subsample volume (vol_j.) The mean and variance of each of these groups were calculated in the usual way. The mean individual dry weight and variance in individual dry weight of all zooplankton were then calculated from these group means and variances as follows.

Because the each group was sampled over a different volume the mean individual dry weight (MDW) was calculated as the weighted sum:

$$\overline{X}=\frac{\sum_{j=1}^{4}\frac{1}{vol_j}\sum_{i=1}^{N_j}X_i}{\sum_{j=1}^{4}\frac{N_j}{Vol_j}} \qquad (1)$$

Which can be written in terms of the group means

$$\overline{X_j}=\frac{\sum_{i=1}^{N}X_{ji}}{n} \qquad (2)$$

as:

$$\overline{X}=\frac{\sum_{j=1}^{4}\frac{N_j}{Vol_j}\overline{X_j}}{\sum_{j=1}^{4}\frac{N_j}{Vol_j}} \qquad (3)$$

The variance in zooplankton dry weight (VDW) was also calculated using a similar weighted variance expression:

$$S^2=\frac{\sum_{j=1}^{4}\frac{1}{vol_j}\sum_{i=1}^{N_j}(X_{ij}-\overline{X})^2}{\sum_{j=1}^{4}[\frac{N_j}{vol_j}]-1} \qquad (4)$$

which can be expanded as:

$$S^2=\frac{\sum_{j=1}^{4}\frac{1}{vol_j}[\sum_{i=1}^{N_j}X_{ij}-2\overline{X}\sum_{i=1}^{N_j}X_{ij}+N_j\overline{X}^2]}{\sum_{j=1}^{4}[\frac{N_j}{vol_j}]-1} \qquad (5)$$

Now, note that the group variances can be written as:

$$S_j^2=\frac{\sum_{i=1}^{N_j}(X_{ij}-\overline{X_j})^2}{N_j-1} \qquad (6)$$

or,

$$S_j{}^2=\frac{\sum_{i=1}^{N_j}X_{ji}^2-\frac{1}{N_j}(\sum_{i=1}^{N_j}X_{ji})^2}{N_j-1} \qquad (7)$$

Using eqn (7), the variance in individual dry weight can then be written in terms of the group means and variance and the mean individual dry weight as:

$$S^2=\frac{\sum_{j=1}^{N_j}\frac{1}{vol_j}[(N_j-1)S_j^2+\frac{1}{N_j^3}\overline{X_j}-2\overline{X}N_j\overline{X_j}+4\overline{X}^2}{\sum_{j=1}^{N_j}\frac{N_j}{vol_j}} \qquad (8)$$

APPENDIX C- Bottom Up Relationships: Summary of the results for normality and homoscedasticity tests for simple linear regressions found in Table 3a. Refer to Table 3a.

Indep Var	Dep Var	Normality [a]	Homoscedasticity[b]
TP	Chl *a*	P = 0.10	0.61[c]
TP	ZB	P > 0.20	0.68
TP	CRB	P = 0.13	0.43
TP	CLB	P > 0.20	0.31
TP	MDW	P > 0.20	n.s.[d]
TP	VDW	P > 0.20	n.s.
Chl *a*	ZB	P > 0.20	0.93
Chl *a*	CRB	P > 0.20	0.46
Chl *a*	CLB	P = 0.08	0.15
Chl *a*	MDW	P > 0.20	n.s.
Chl *a*	VDW	P > 0.20	0.19

[a] The Kolmogorov-Smirnov test for normality was used.

[b] The Levene Median test for equality of variances was used.

[c] If the result is greater than 0.05, the residuals meet the normality and homoscedasticity criterion.

[d] If the result is less than 0.05, the residuals do not meet the normality and homoscedasticity criterion.

APPENDIX D- Bottom Up Relationships: Summary of the results for the power analysis on simple linear regressions found in Table 3a. Refer to Table 3a. Power has only been calculated for those relationships that were found not to be significant

Indep Var	Dep Var	Power[a]
TP	ZB	0.031
TP	CRB	0.081
TP	CLB	0.081
Chl *a*	ZB	0.242
Chl *a*	CRB	0.375
Chl *a*	CLB	0.427

[a] Power is defined as the probability that the model correctly describes the relationship of the variables, if there was a relationship (SigmaStat User's Manual, 1992).

APPENDIX E- Top-Down Relationships: Summary of the results for normality and homoscedasticity tests for One-Way ANOVA's found in Table 4a. Refer to Table 4a.

Indep Var	Dep Var	Normality	Homoscedasticity
PFISH	Chl *a*	P > 0.20	P = 0.23
PFISH	ZB	P > 0.20	P = 0.64
PFISH	CRB	P > 0.20	P = 0.97
PFISH	CLB	P > 0.20	P = 0.96
PFISH	MDW	P > 0.20	P = 0.41
PFISH	VDW	P > 0.20	P = 0.17

**Refer to Appendix C.

APPENDIX F- Top-Down Relationships: Summary of the results for the power analysis on the One-Way ANOVA's found in Table 4a. Refer to Table 4a. Power has only been calculated for those relationships that were found not to be significant.

Indep Var	Dep Var	Power
PFISH	Chl *a*	[a]
PFISH	ZB	0.05
PFISH	CRB	0.20
PFISH	MDW	0.17

[a] Power is defined as the probability that the test will detect a difference among groups if there really is a difference (SigmaStat User's Manual, 1992).

APPENDIX G.1- Morphometric and physico-chemical data measured in the 29 lakes measured during the first sampling period. (Date= Julian Date; Max Depth= Maximum depth (metres); Mean depth (metres); Secchi depth (metres); pH ; Temp= Temperature (Celcius); Cond= Conductivity (µmhos cm^{2}). N.A. represents measurements which were not available.

Lake	Date	Max Depth	Mean Depth	Secchi Depth	pH	Temp	Cond
Big	199	95	12.3	5.25	8.58	23.56	211.9
Black	176	9.45	3.13	3.9	7.55	20.18	81
Brown	179	10	5.2	3.5	7.79	23.98	68.17
Carmen	179	3.6	1.3	4	7.67	24.15	64.25
Croche	206	10.5	8.5	5.1	6.56	20.83	22.5
Cromwell	205	8	3.04	2.9	6.48	22.25	22.25
Fortune	178	22.5	3.99	3.1	7.59	22.63	22.63
Geai	205	N.A.	N.A.	3	5.98	19.85	18.2
Gould	218	61.5	21.9	6.75	8.57	22.91	173
Harringt.	163	21	9.45	5	7.84	21.8	70.33
Kidder	212	14.6	6.8	6	7.59	21.21	55
Kingsmere	197	9.76	3.97	7	8.04	21.71	144.5
Lower	198	26	9.2	4.7	8.57	23.36	259
La Pèche	173	32	5.59	5.1	8.15	20.5	99.57
Le Blanc	175	9	5.2	4	7.59	21.56	54.6
Loutre	194	3.6	1.5	3.5	8.23	21.63	140.75
Meech	164	22.2	9.9	8	7.74	18.07	83.88
Mulvihill	211	3.65	1.12	2.5	7.91	22.85	158.17
Opinicon	213	9.15	4.9	3.1	8.47	24.15	186.78
P. Renaud	177	1.8	0.6	1.5	7.75	24	100
Philippe	169	17.4	8.69	5	7.89	19.36	75.86
Pin Rouge	207	14	8.7	3.5	7.41	21.72	57.8
Ramsey	175	9.5	4.12	2.5	7.48	19.38	53.67
Renaud	177	4.3	0.96	3	7.49	22.05	81.57
Sydenham	218	37	6.8	5	8.73	22.32	236.5
Taylor	171	12.2	4.67	5.4	7.95	21.23	81.58
Triton	206	3.2	2.15	2.75	6.43	24	25
Upper	198	7	2.4	3.75	8.37	24.87	273.33
Vase	196	5	1.9	3.3	7.4	21.38	63.4

APPENDIX G.2- Morphometric and physico-chemical data measured in the 29 lakes measured during the second sampling period. (Date= Julian Date; Secchi depth (metres); pH ; Temp= Temperature (Celcius); Cond= Conductivity (μmhos cm^2). N.A. represents measurements which were not available.

Lake	Date	Secchi Depth (m)	pH	Temp	Cond
Big Rideau	239	5.25	8.49	21.78	201
Black	221	3.75	7.66	20.42	91.7
Brown	241	2.5	7.73	18.57	82
Carmen	235	2.8	7.76	22.2	N.A.
Croche	243	5	6.58	18.15	21.1
Cromwell	254	7.25	6.49	19	23
Fortune	229	4	7.76	21.54	21.5
Geai	N.A.	N.A.	N.A.	N.A.	N.A.
Gould	N.A.	N.A.	N.A.	N.A.	N.A.
Harringt.	220	7	7.76	22.02	79.2
Kidder	234	6.9	7.64	21.43	55.3
Kingsmere	233	4.75	8.23	22	151
Lower Bev.	231	3.2	8.48	21.73	253
La Pèche	227	5.5	8.48	23.45	109
Le Blanc	225	6.1	7.65	21.03	63.5
Loutre	241	3.25	8.59	22.5	144
Meech	197	7	8.12	22.48	89.9
Mulvihill	233	2.9	7.92	22	150
Opinicon	240	3.75	8.54	22.54	178
P Renaud	228	1	7.92	24.2	117
Philippe	219	6	7.9	21.56	80.8
Pin Rouge	255	3.75	6.89	18.33	138
Ramsey	224	3.75	7.13	20.4	62
Renaud	228	3.1	7.02	22.16	81.3
Sydenham	242	5.3	8.77	21.92	232
Taylor	219	5	7.92	22.43	87.4
Triton	254	3	6.77	19	21.3
Upper Bev.	231	3	8.4	23	273
Vase	234	3.25	7.44	21.6	105

APPENDIX G.3- Chlorophyll *a* concentrations, total phosphorous concentration, fish presence, index of fish abundance, and zooplankton biomass data measured during the first sampling period. Chlorophyll *a* size classes= Net >35 μm, 12<Micro<35 μm, 0.2<Nanno<12 μm, Pic<0.2 μm; TChl *a*= total chlorophyll *a* concentration (μg $litre^{-1}$); PFISH= presence (1) or absence (0); PFA= piscivorous fish abundance index (catch per 48 hr effort); ZB= zooplankton biomass (μg dry weight $litre^{-1}$); COB= copepod biomass (μg dry weight $litre^{-1}$); CLB= cladoceran biomass (μg dry weight $litre^{-1}$); NAB= naupli biomass (μg dry weight $litre^{-1}$); ROB= rotifer biomass (μg dry weight $litre^{-1}$). N.A. represents measurements which were not available.

Lake	Net	Micro	Nann	Pico	TChl*a*	TP	PFIS	PFA	ZB	COB	CLB	NAB	ROB
Big Rideau	0.248	0.191	0.783	2.682	3.905	17.44	1	N.A.	288.915	58.334	209.115	14.930	6.535
Black	0.298	0.279	0.712	1.667	2.777	12.95	0	0	59.972	8.421	29.551	8.733	13.267
Brown	0.547	0.348	2.848	5.874	8.905	23.41	1	44	37.321	5.265	11.695	1.320	19.041
Carmen	0.252	0.336	0.786	1.761	3.135	23.04	1	146	162.220	81.789	11.987	1.693	66.750
Croche	0.216	0.121	0.685	0.262	1.284	5.79	1	N.A.	131.092	7.932	107.979	3.341	11.840
Cromwell	0.245	0.203	1.655	1.812	3.914	12.52	1	N.A.	160.376	41.252	103.234	3.373	12.517
Fortune	0.308	0.226	0.594	1.520	2.648	17.00	0	0	250.875	135.435	68.764	19.505	27.171
Geai	0.106	0.155	1.140	2.260	3.661	10.15	0	0	173.420	25.880	72.057	4.299	71.185
Gould	0.124	0.287	0.637	0.360	1.407	6.79	1	N.A.	303.166	237.776	60.895	3.415	1.079
Harringt.	0.206	0.120	0.379	1.226	1.930	5.92	1	143	N.A.	N.A.	N.A.	N.A	N.A
Kidder	0.000	0.080	0.526	0.441	1.038	5.73	0	0	116.873	31.915	73.572	0.000	11.387
Kingsmere	0.245	0.143	0.660	1.300	2.348	11.21	0	0	269.155	74.873	141.100	5.691	47.491
Lower Bev.	0.339	0.392	0.000	3.645	4.376	24.91	1	N.A.	270.739	152.431	99.352	12.030	6.926
La Pèche	0.121	0.202	0.541	1.385	1.978	10.71	1	595	243.611	108.852	109.369	11.564	13.826
Le Blanc	0.133	0.609	0.407	0.827	1.974	7.54	1	109	620.907	252.555	352.890	12.618	2.844
Loutre	0.203	0.138	1.217	0.190	1.855	15.44	1	118	199.689	62.033	113.835	13.721	10.100
Meech	0.171	0.047	0.465	0.826	1.392	6.10	1	167	237.289	172.877	51.090	9.943	3.379
Mulvihill	0.533	0.293	1.094	2.560	4.481	18.49	0	0	333.081	35.046	64.786	175.232	58.016
Opinicon	2.787	0.527	1.460	1.944	6.719	24.47	1	N.A.	176.360	69.059	57.730	18.131	31.439
P. Renaud	0.150	0.227	0.000	1.070	1.800	16.13	0	0	2.746	0.211	1.163	0.327	1.045
Philippe	0.136	0.130	0.652	0.865	1.620	8.91	1	16	231.715	187.697	15.248	7.027	21.743
Pin Rouge	4.046	0.226	1.030	2.112	8.127	11.77	1	N.A.	104.348	43.816	52.817	4.243	3.472
Ramsey	0.249	0.303	1.432	1.901	3.886	14.51	0	0	275.187	35.722	220.861	5.056	13.547
Renaud	1.135	0.181	1.313	0.825	3.455	21.23	1	112	597.898	194.270	322.948	19.317	61.363

Sydenham	3.319	0.437	1.292	0.000	4.505	19.55	1	N.A.	488.842	247.593	228.150	7.928	5.171
Taylor	0.070	0.228	0.716	0.889	2.218	8.78	1	413	198.208	173.204	19.136	2.855	3.014
Triton	0.173	0.155	0.687	0.608	1.622	10.65	0	0	93.348	6.281	64.083	4.067	18.917
Upper Bev.	0.414	0.224	0.660	1.750	3.048	14.07	1	N.A.	166.074	45.174	98.064	11.295	11.541
Vase	0.150	0.220	0.903	2.567	3.785	15.44	0	0	187.334	28.816	101.438	38.479	18.601

APPENDIX G.4- Chlorophyll *a* concentrations, total phosphorous concentration, fish presence, index of fish abundance, and zooplankton biomass data measured during the second sampling period. Chlorophyll *a* size classes= Net >35 µm, 12<Micro<35 µm, 0.2<Nanno<12 µm, Pic<0.2 µm; TChl *a*= total chlorophyll *a* concentration (µg $litre^{-1}$); PFISH= presence (1) or absence (0); PFA= piscivorous fish abundance index (catch per 48 hr effort); ZB= zooplankton biomass (µg dry weight $litre^{-1}$); COB= copepod biomass (µg dry weight $litre^{-1}$); CLB= cladoceran biomass (µg dry weight $litre^{-1}$); NAB= naupli biomass (µg dry weight $litre^{-1}$); ROB= rotifer biomass (µg dry weight $litre^{-1}$). N.A. represents measurements which were not available.

Lake	Net	Nann	Micro	Pico	TChl*a*	TP	ZB	COB	CLB	NAB	ROB
Big Rideau	0.383	0.995	0.355	1.675	3.409	15.195	75.130	17.067	34.605	16.098	7.361
Black	0.371	1.898	0.596	3.567	6.432	15.008	49.940	1.752	36.998	3.120	8.069
Brown	3.082	4.920	9.944	1.569	19.515	26.464	94.409	5.537	51.044	15.380	22.448
Carmen	1.942	4.158	3.333	1.470	10.903	31.009	55.445	19.981	20.123	4.645	10.696
Croche	2.021	2.328	0.325	0.000	3.929	6.042	44.482	12.362	20.912	2.736	8.473
Cromwell	0.595	4.097	0.773	1.957	3.775	14.323	31.279	14.291	0.000	0.000	16.988
Fortune	1.469	1.039	0.516	1.445	4.469	14.136	263.705	187.219	59.201	5.439	11.847
Geai	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Gould	N.A.	N.A.	N.A	N.A	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Harringt.	0.252	0.288	0.195	0.948	1.682	8.844	138.996	49.293	25.430	62.393	1.880
Kidder	1.066	0.520	0.183	0.000	1.612	5.300	56.461	9.453	42.474	2.782	1.752
Kingsmere	0.270	0.961	0.255	0.712	2.198	8.284	156.119	15.455	109.421	29.800	1.443
Lower Bev.	0.440	1.810	0.473	2.921	5.644	20.860	158.700	38.895	92.294	19.279	8.233
La Pèche	0.280	0.844	0.299	0.819	2.242	8.968	132.501	40.599	79.321	8.720	3.861
Le Blanc	0.206	0.407	0.188	0.418	1.219	5.420	74.028	13.582	49.699	9.187	1.559
Loutre	0.451	1.559	0.366	0.869	3.442	16.938	89.615	15.231	56.244	10.721	7.419
Meech	0.143	0.590	0.094	0.673	1.499	5.918	137.243	92.189	40.001	2.785	2.268
Mulvihill	2.450	2.397	0.893	0.853	6.593	21.732	174.127	27.853	76.971	13.773	55.530
Opinicon	1.386	1.442	0.820	2.018	5.666	19.802	90.708	27.119	43.431	13.640	6.517
P Renaud	0.326	1.479	0.687	0.440	2.851	15.008	8.786	0.000	6.619	1.587	0.580
Philippe	0.923	0.807	0.312	1.032	2.843	10.587	257.064	131.491	114.627	1.454	9.491
Pin Rouge	2.170	1.884	0.496	0.987	5.537	11.023	62.833	12.221	42.469	3.158	4.986
Ramsey	0.940	1.450	0.421	2.598	5.408	12.455	89.029	18.584	61.011	3.131	6.303
Renaud	3.650	2.421	1.002	0.000	5.526	26.153	217.779	15.368	98.703	14.769	88.939
Sydenham	3.921	0.651	0.419	0.919	5.910	12.829	176.617	57.048	101.414	9.858	8.297
Taylor	0.202	0.844	0.483	1.172	2.579	8.844	193.453	128.430	38.275	15.075	11.674

Triton	0.180	0.920	0.072	1.617	2.753	9.529	16.969	0.339	8.841	1.939	5.850
Upper Bev.	0.075	1.718	0.796	3.697	6.286	17.249	120.572	2.757	90.024	11.917	15.874
Vase	0.539	2.267	0.666	3.737	7.210	17.872	142.137	23.950	84.462	19.270	14.455