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Author(s): Bernadette PINEL-ALLOUL, Théophile NIYONSENGA and Pierre LEGENDRE
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Spatial and environmental components of freshwater zooplankton structure[1]

Bernadette PINEL-ALLOUL, Théophile NIYONSENGA[2] & Pierre LEGENDRE, GRIL, Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre ville, Montréal, Québec H3C 3J7, Canada.

Abstract: Paradigms based upon physical and geochemical bottom-up processes or trophic cascade/top down theory have been developed to explain heterogeneity of freshwater zooplankton, but these paradigms taken alone seem unable to encompass the full range of zooplankton variability and have led to controversy. The goal of the study is to test the hypothesis that both abiotic and biotic environmental factors, and spatial structuring, explain simultaneously the large-scale spatial heterogeneity of freshwater zooplankton in Québec lakes. Partial Canonical Correspondence Analysis (Partial CCA) was used to partition the variance of zooplankton species abundances into independent components: a) non-spatial environmental factors (physics, chemistry, morphometry, phytoplankton and fish communities), b) spatial component of environmental influence, c) pure spatial factors (geographic coordinates), and d) undetermined. Our study shows that pure and spatially-structured abiotic and biotic environmental factors (a+b) explain 48% of the variation of zooplankton within Québec lakes. Our study supports the multiple driving forces hypothesis and shows that the control model of the zooplankton structure within Québec lakes includes both abiotic factors (mainly related to the water chemistry gradients) and biotic bottom-up (phytoplankton) and top-down (fish) factors. Across our large geographic scale, the abiotic factors, especially those related to water chemistry, are the main environmental processes explaining zooplankton community structure variability within Québec. Pure spatial factors (c) have small and nonsignificant contribution (8%) to zooplankton variation. The large amount of unexplained variation (d: 44%) suggests that other external factors, operating at local scales and not taken into account in this study, can exert influence on lake zooplankton structure.

Keywords: zooplankton, Québec lakes, spatial heterogeneity, bottom-up factors, top-down factors, partial canonical correspondence analysis, ecological modelling, spatial analysis.

Résumé: Des paradigmes basés soit sur les processus physiques et géochimiques ascendants, soit sur les interactions trophiques en cascade et les processus descendants ont été développés pour expliquer l'hétérogénéité du zooplancton d'eau douce. Toutefois, ces paradigmes pris seul à seul n'expliquent pas toute la variabilité du zooplankton et ils ont fait l'objet de controverses. Le but de cette étude est de tester l'hypothèse selon laquelle les facteurs écologiques tant abiotiques que biotiques, ainsi que la structure spatiale, expliquent conjointement l'hétérogénéité spatiale à grande échelle du zooplancton dans les lacs du Québec. L'analyse canonique partielle des correspondances a permis de fractionner la variance dans la composition et l'abondance du zooplancton selon quatre composantes: a) la composante environnementale pure, non-spatialement structurée (physico-chimie, morphométrie, phytoplancton, communauté de poissons), b) la composante environnementale spatialement structurée, c) la composante spatiale pure (coordonnées géographiques), et d) la composante indéterminée. Notre étude démontre que les effets purs et spatiaux des facteurs environnementaux d'origine abiotique et biotique (composantes a + b) expliquent 48% de la variation du zooplankton dans les lacs du Québec. Notre étude vient appuyer l'hypothèse du contrôle multiple des communautés; le modèle de contrôle environnemental de la structure du zooplancton dans les lacs du Québec comprend à la fois des facteurs abiotiques reliés aux gradients physico-chimiques et des facteurs biotiques ascendants (phytoplancton) et descendants (communauté de poissons). A grande échelle géographique, les facteurs abiotiques reliés à la physico-chimie des eaux sont les principaux facteurs expliquant la variabilité dans la structure des communautés de zooplancton au Québec. La composante spatiale pure (c) n'a qu'une faible contribution non significative (8%) à la variabilité du zooplancton. La forte proportion de variance inexpliquée (d: 44%) suggère que d'autres facteurs externes, opérant à l'échelle locale et qui n'ont pas été pris en compte dans le cadre de cette étude, peuvent exercer une influence sur la structure du zooplancton lacustre.

Mots-clés: zooplancton, lacs du Québec, hétérogénéité spatiale, facteurs ascendants, facteurs descendants, analyse canonique partielle des correspondances, modélisation écologique, analyse spatiale.

Introduction

A perennial theme confronting investigators of both terrestrial and aquatic ecosystems concerns the regulation of living communities and the extent to which physical, chemical, or biological factors dominate or interact as controlling forces (Lehman, 1991). It is now recognized that populations and communities of organisms are influenced by a host of abiotic and biotic factors, and it has been suggested that the relative role of different ecological forces should vary among biological systems, and even within the same system (Hunter & Price, 1992). Thus, one of the major challenges for the discipline of ecology is to measure the relative strengths of these factors in natural ecosystems, untangle the interactions among them, and so explain the patterns of animal and plant distribution and abundance in nature. In planktonic systems, paradigms based upon physical and geochemical bottom-up processes (Pinel-Alloul *et al.*, 1990a; 1990b; Mollot & Dillon, 1991; Chow-Fraser, 1991; Duarte, Augusti & Canfield, 1992; Nicholls, Nakamoto & Keller, 1992), trophic cascade/top-down theory (McQueen, Post & Miller, 1986; Mazumder *et al.*, 1990; Lazzaro *et al.*,

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[2] Present address: CHUS/CRC/DSSC/FAMUS, Université de Sherbrooke, 3001, 12e avenue Nord, Sherbrooke, Québec J1H 5N4, Canada.

1992; Kitchell, 1992) and within-lake or replicate sample heterogeneity (Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991; Kolasa & Pickett, 1991; Downing, 1991) have been developed to explain plankton variance, but these factors taken alone seem unable to encompass the full range of plankton variability and lead to controversy (DeMelo, France & McQueen, 1992; Carpenter & Kitchell, 1992). In the eighties, the debate contrasted two important paradigms. On the one hand, the environmental control model, which involves regulation by "bottom-up" processes, suggested a dominant role for physical and chemical factors (nutrients, water turnover time, water chemistry, lake morphometry, watershed geology and use), especially along environmental trophic gradients or in nutrient-limited ecosystems (Peters, 1986; Pace, 1986; Prairie, Duarte & Kalf, 1989; Downing & McCauley, 1992). On the other hand, tenants of the biotic control model considered the trophic interactions among organisms such as predation ("top-down" processes) and competition to be the primary factors structuring planktonic communities (Mazumder *et al.*, 1990; Sommer, 1989; Carpenter & Kitchell, 1988; Vanni, 1988). Critical reviews of these paradigms (McQueen, Post & Mills, 1986; Hunter & Price, 1992; Power, 1992) concluded that "bottom-up" and "top-down" forces may act on populations and communities simultaneously and that the dominant forces will vary within and among systems according to sampling scales. With a few notable exceptions (Carpenter & Kitchell, 1988; Mazumder *et al.*, 1988, Rodriguez, Magnan & Lacasse, 1993), there has been to date little assessment of the relative roles of these different ecological forces in determining plankton community structure. Therefore, the relative importance of these factors in determining zooplankton community structure remains to be explored and tested.

Ecologists have taken many approaches to examine the factors that explain population change and community composition, from empirical (Peters, 1986), theoretical (Cohen & Newman, 1988) or mechanistic and descriptive approaches (Lehman, 1986). All of these approaches have proven valuable, and they often feed on one another. However, most of these approaches attempt to model the observed variation in patterns and processes of natural communities in terms of a single type of cause. Quinn & Dunham (1983) and more recently Power (1992) proposed a different way to understand and model natural communities, by considering the contributions of alternative (non-mutually exclusive) processes, and their relative strengths along productivity gradients or predator-prey functional responses. A quantitative statistical approach to this problem has recently been proposed by Borcard, Legendre & Drapeau (1992), which partitions the variation of species assemblages and allows one to measure the relative contribution of sets of explanatory variables. This method is conceptually linked to the idea that ecological heterogeneity in natural communities is explained by non-mutually exclusive abiotic and biotic factors that overlap in space and time.

The present study combines spatial, abiotic and biotic explanatory variables into a single model to analyze large-scale patterns of variation in zooplankton community structure in Québec lakes. Despite an enormous literature on zooplankton (species-environment) patterns, few studies have yet combined these three general categories of explanatory factors. In 1982, the Department of the Fisheries and Oceans (Environment Canada) initiated a large-scale survey program to assess water quality in more than 200 lakes in areas of Québec which are most sensitive to the Long Range Transport of Air Pollutants (LRTAP) (Langlois *et al.*, 1983). Among them, the biological communities (phyto-and zooplankton, benthos and fish) of 54 lakes were assessed in order to relate community structure to lake's acidification status. This survey offered us an unequaled opportunity to evaluate the relative importance of the different processes controlling the spatial patterns of variability in the zooplankton communities of Québec lakes against a framework of large geographic scale and water chemistry gradients. In the present paper, we consider two main hypotheses. First, we test the multiple forces hypothesis that both the environmental abiotic and biotic factors, as well as independent spatial structuring processes, explain zooplankton composition and abundance variability. Second, we examine the hypothesis that the abiotic factors (water quality and lake morphometry) are the most important processes to explain large-scale variation in the zooplankton community. The various sets of factors, abiotic (physics, chemistry and morphometry) and biotic (phytoplankton and fish), will be investigated in a nested manner in order to determine the minimal set of variables explaining as much as possible of the large-scale zooplankton spatial variability. We will use the quantitative statistical approach of variance partitioning developed by Borcard, Legendre & Drapeau, (1992) using Partial Canonical Correspondence Analysis to give a clear assessment of the effects of various sets of environmental factors, partialling out the spatial component of the zooplankton community data set. Since the only earlier study (Rodriguez, Magnan & Lacasse, 1993) attempting to prove the multiple forces hypothesis on freshwater zooplankton structure was done over a small regional scale and was limited to cladoceran species assemblages, the present study represents a first attempt at developing a method of analysis and a model of the spatial variation in the total zooplankton community based on multiple processes and over a large geographic scale.

Methods

STUDY AREA

Fifty-four lakes were sampled throughout the Laurentian Shield, north of the St. Lawrence river and south of latitude 52° N (Figure 1). Details on geographic locations, and on the morphometric, physical and chemical characteristics of the lakes, have been presented by Pinel-Alloul *et al.* (1990a). Most of the lakes chosen were summer-stratified, easily accessible, and not affected by human or agricultural activity in their immediate watershed. A southwest-to-northeast geographic gradient in acidity and aluminium concentration, and a reverse gradient in sulphate and alkalinity, were detected (Pinel-Alloul, Méthot & Codin Blumer, 1987). Seventy-two per cent of these lakes exhibited acid neutralizing capacity (ANC) less than 100 $\mu eq \bullet L^{-1}$ and had an alkalinity/sulphate ratio lower than one, indicating an extreme sensitivity to acidification (Bobée & Lachance,

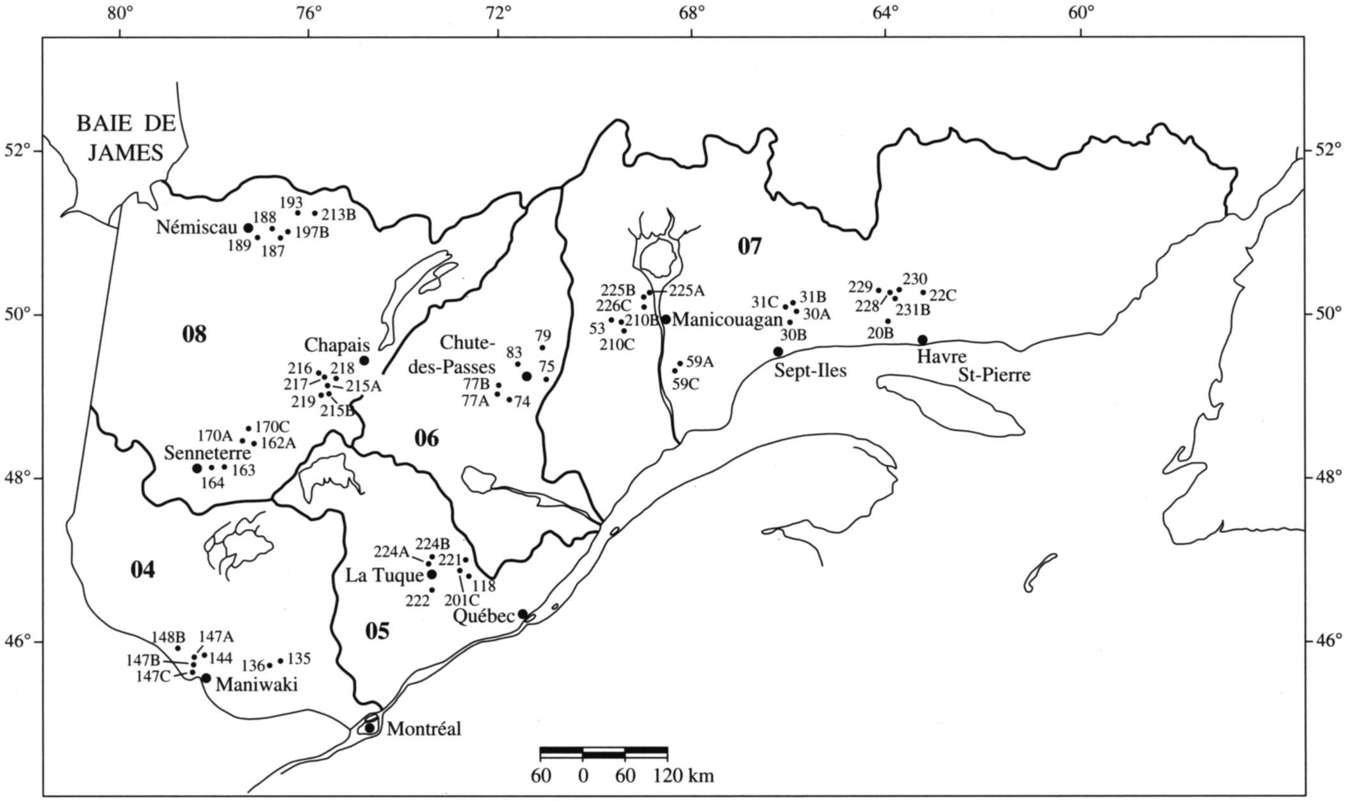


FIGURE 1. Geographic location of the study lakes in Québec. Numbers refer to lakes within each geographical area.

1984). A preliminary study, based on abiotic variables, showed that five composite factors explained 73% of the total environmental variability in water chemistry and morphometry among lakes (Pinel-Alloul & Méthot, 1985; Pinel-Alloul *et al.*, 1990b). These composite factors can be classified into two categories that represent the main environmental gradients related to the north-east to south-west geographic axis: on the one hand, positive values for the hardness-alkalinity factor (21%) and the salinity-sulphate factor (10%) are characteristic of the southwestern lakes, and on the other hand, positive values for the lake depth and water transparency factor (17%), the dystrophy factor (14%), and the lake size factor (11%) characterize lakes in the northeastern and central regions.

FIELD AND LABORATORY ANALYSES

The environmental variables were investigated between August 11th and September 18th, 1982, and comprise 12 morphometric and 20 physical and chemical variables (Appendix 1). The methods used to estimate lake morphometry and water quality variables are fully described in Pinel-Alloul *et al.*, (1990a, 1990b). The chemical analyses and the estimation of the acid neutralizing capacity (ANC: $\mu eq \bullet L^{-1}$) followed Kramer (1980) and Bobée *et al.* (1982). In order to minimize seasonal variations in plankton and fish communities during the survey of the lakes over this large geographic scale, sampling was carried out by hydroplane within one month (July 9 to August 10, 1982). Zooplankton sampling was limited to a unique composite zooplankton sample per lake collected at the site of maximum depth during summer stratification except in four shallow lakes (maximum depth: 4m). This composite sample was obtained by means of a Wisconsin net (20.5 cm in diameter, 64-µm mesh) which was towed vertically several times at depths ranging from 2 to 20 m (= maximum volume filtered of 63 to 628 liters, but the filtration efficiency was not measured) depending on the maximum depth of the lake. This sampling procedure enabled us to estimate quantitatively the micro- (rotifers, nauplii, small cladocerans) and the macro-zooplankton (copepods, large cladocerans) components. Animals were concentrated in 200-500 mL and preserved upon collection in 9% formalin with sucrose. Laboratory procedures for zooplankton counting and analysis are described by Pinel-Alloul *et al.* (1990a). A total of 54 zooplankton taxa (21 Rotifera, 18 Cladocera, 8 Calanoida, 6 Cyclopoida, and the nauplii of Copepods) were identified (Appendix 2). The zooplankton was counted in 10 mL subsamples using a counting wheel and their densities were expressed as number of individuals per cubic meter. Phytoplankton integrated samples were collected by immersing a 2.4-cm diameter, 5 m long flexible PVC tube in epilimnetic waters (5 m). Acidified Lugol's iodine solution was added immediately to preserve the samples for quantitative analysis. Laboratory procedures and phytoplankton species analysis are described in Pinel-Alloul *et al.* (1990b). A total of 87 phytoplankton taxa and groups were identified (Appendix 2) and their counts expressed in cells per mL. Fish were caught using an experimental multifilament gillnet (47.7-m long with streched mesh of 3.8-, 5.1-, 6.4-, 7.6-, 8.9- and 10.2-cm) which was set randomly over the whole lake. The fish species were identified on the spot and fish abundances were expressed as numbers captured per effort unit (22 hours per lake). A total of 18 species and groups were caught (Appendix 2), although only 8 species were discriminant for the fish community typology: 3 salmonids (*Salvelinus fontinalis*, *S. namaycush*, *Coregonus clupeaformis*), 2 catastomids (*Catostomus commersoni*, C. *catostomus*), 2 percids (*Perca flavescens*, *Stizostedion vitreum*) and 1 esocid (*Esox lucius*) (Pinel-Alloul & Méthot, 1985).

STATISTICAL ANALYSES

The methods used to substantiate our hypotheses are Canonical Correspondence Analysis (CCA) and Partial Canonical Correspondence Analysis (Partial CCA) (ter Braak, 1986; 1988). Recently, Palmer (1993) demonstrated that the CCA performs quite well with skewed species distributions and with highly intercorrelated environmental variables. Borcard, Legendre & Drapeau (1992) derived from partial CCA a method allowing to single out the respective effects of the environmental factors and of the spatial structure of the samples. The among-lake variation in species composition can be partitioned into independent components: (a) a fraction that is attributed to the non-spatially-structured part of the environmental variables (abiotic, biotic, or both); (b) a second fraction explained by the spatially-structured part of these environmental variables; (c) a pure spatial component, unexplained by any of the environmental variables included in the analysis, which may reflect some process generating spatial heterogeneity such as biogeographical distribution, or behavioral factors, or else other spatially-structured physical or biological processes not included in the analysis; and (d) a fraction of the species variation that remains unexplained by the spatial coordinates or the environmental variables. In this analysis, the amount of spatially-structured zooplankton variation which is unaccounted for by the factors under study (c) will be taken as a measure of the existence of variables that are spatially-structured and important in determining zooplankton distribution, but that have not been included yet in the explanatory model. If these factors are environmental, they can be measured further and included in the model; if they are of biogeographical and historical nature (biogeography, dispersal history, *etc.*: see Borcard & Legendre, 1993 for a discussion), it may be more difficult to explicitly include them in the analysis.

Before the analysis, all species that occurred in fewer than three sampled lakes in the zooplankton data matrix, and five sampled lakes in the phytoplankton data matrix, were eliminated from the data tables. For the fish data matrix, we only retained the 8 discriminant species previously retained by a correspondence analysis. The problem of missing abiotic data (2 sites for morphometric data) was handled by a statistical procedure explained in Mirkin (1990), and available in the statistical analysis package developed by Mirkin & Yeriomin (1991). The method consists of finding, by an iterative procedure, the estimated values that change as little as possible the principal component structure of the data matrix.

When performing canonical analysis, a linear model is assumed for all relationships between the independent and dependent variables, although in CCA the dependent data table is first subjected to the correspondence analysis transformation, prior to looking for these linear relations; so, one would like all relations between independent variables (phytoplankton and fish species abundances, physical and chemical variables, morphometry) and transformed dependent variables (zooplankton species abundance) to be linear, as explained in ter Braak (1987). This assumption was not met by the phytoplankton and fish variables, which displayed unimodal species distributions along the environmental gradient; this is usual in data that cover a large geographic scale, as is the case in the present study. To meet the linearity assumption of canonical analysis, the phytoplankton and fish data matrices were transformed in such a way that a correct ordination of the sites and the species along environmental gradients would be obtained by principal component analysis. The following transformation was used (Legendre & Legendre, 1983):

$$q_{ik} = p_{ik} / (p_i + \sqrt{p_{+k}}) \qquad [1]$$

where p_{ik} is the frequency f_{ik} of species i in lake k divided by the total sum of frequencies in the whole data table f_{++}; p_{i+} is the sum of values in row i of the table divided by f_{++}, and p_{+k} is the sum of values in column k divided by f_{++}. Following this transformation, a principal components analysis of the matrix values would preserve the chi-square distance among rows (and columns) of the original data table (Legendre & Legendre, 1983).

For the CCA and Partial CCA analyses, the independent environmental matrices finally include 12 morphometric variables, 20 physical and chemical characteristics, 61 phytoplankton taxa, and 8 fish species, for a total of 101 variables (independent variables marked with an asterisk in Appendices 1 and 2). The dependent zooplankton data matrix consists of 38 taxa (14 Rotifera, 12 Cladocera, 6 Calanoida, 5 Cyclopoida, and the nauplii of Copepods) (taxa marked by an asterisk in Appendix 2). Many of the independent variables display relationships among them (collinearity). Indeed, the physical and chemical characteristics and the morphometric variables (abiotic factors) are likely to have some influence on the phytoplankton and fish communities (biotic factors). Table I shows for instance that the physical and chemical characteristics explain about 62% of the total variability in the morphometric factors, about 48% of the total variation in the fish community and 38% of the total variation in the phytoplankton taxa. Morphometric variables also were related, to a lesser extent, to the phytoplankton and fish communities (respectively 23 and 31% of their total variation). Phytoplankton and fish communities seem less correlated (12.4%). Because of the large number of independent variables and sampling sites involved in the analysis, a forward selection procedure was used to find the smallest set of environmental variables that explain the zooplankton community about as well as the full set. At each step, the variable is selected that adds the most to the

TABLE I. Relationships among the different independent environmental factor sets: proportion of the dependent variables variation explained by canonical correlations

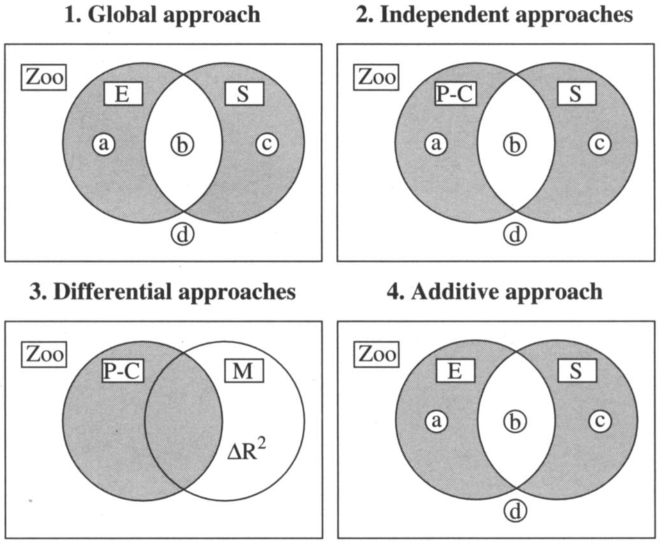
Sets of environmental variables	Morphometry	Phytoplankton	Fish
Physical and chemical	61.9%	37.91%	47.58%
Morphometry	—	22.96%	30.81%
Phytoplankton		—	12.39%

explained variability in the species data (Montgomery & Peck [1982] and ter Braak [1990]). However, in each set of factors, variables may show strong inter-correlations. Several of them may then display equal variance contribution to the total variation in species composition (zooplankton taxa), but only one will be chosen by the forward selection procedure; so, the best subset of environmental variables, in terms of the variables exerting more influence on the zooplankton (obtained by the forward selection procedure), is not unique (Montgomery & Peck, 1982).

The matrix of spatial factors was constructed as suggested by Legendre (1990), involving a polynomial of the geographic coordinates (x,y). Since the position of the lakes was given in longitudes and latitudes, a series of transformations involving measurement of the distances along the earth's curvature, followed by principal coordinates analysis, were used to obtain Cartesian coordinates (x,y). The coordinates (x,y) were then rescaled in the range -1 to +1 to avoid extremely large or small values of the terms x^2, y^2, x^2y, xy^2, x^3, y^3, etc. (Ripley, 1981). A polynomial of degree 3 had a contribution of 31.2% to the explanation of the total variation in the zooplankton composition ($P = 0.01$). The terms added to attain degree 4 accounted for 9.4% but their contribution was not significant ($P = 0.08$). Following Borcard, Legendre & Drapeau (1992), a forward selection procedure led to retain the terms in x, y, x^2, x^2y, y^3. The contribution of these 5 spatial factors to the explanation of the spatial variation of the zooplankton taxa (which was 22.8% of the total variation of the zooplankton composition) was statistically significant at the Bonferroni-corrected level $P = 0.01$, for a nominal significance level of 5% over 5 simultaneous tests; significance is assessed by a permutation test in CCA.

Four statistical analyses were carried out. (1) A *global approach* was used to test the first hypothesis that abiotic (physics, chemistry and morphometry) and biotic (phytoplankton and fish), as well as the spatial structure, jointly explain the variations in zooplankton community. In this approach, we put all the environmental variables together (the forward selection procedure applied to the 101 environmental variables led to 12 predictors) and outlined their effects on zooplankton composition, controlling for the spatial structure. Figure 2.1 illustrates the global approach; Zoo stands for the total variance in zooplankton community, E for the portion explained by all 12 environmental variables, and S for the portion explained by the 5 spatial variables. Letters (a), (b), (c) and (d) are those used above as well as in Borcard, Legendre & Drapeau (1992) to identify the different fractions of variation.

(2) One may also be interested to test the effect of each set of environmental factors independently. We call these the *independent approaches*. This question was directly addressed by performing Partial CCA independently for each set of environmental variables (physics and chemistry, morphometry, phytoplankton and fish), controlling for space. One of them is illustrated in Figure 2.2, where the zooplankton variation (Zoo) is partitioned among the physical and chemical variables (P-C), on the one hand, and the spatial structure (S) on the other. The forward selection procedure is involved at each step to find the most significant environmental factors.


1. Global approach

2. Independent approaches

3. Differential approaches

4. Additive approach

FIGURE 2. Statistical approaches used in the study to test the effects of abiotic and biotic environmental factors on zooplankton structure. See explanations in text.

(3) Then, one may wonder whether some factors are superfluous, in the sense that their additional influence may be negligible. Figure 2.3 illustrates one of these analyses, that belong to our *differential approaches*: one wonders whether the morphometric factors (M) increase in a significant way the portion of zooplankton variance explained (∂R^2), after the physical and chemical variables (P-C) have been incorporated in the model.

Finally (4), we will use all the significant factors independently determined by the forward selection procedures for the different sets of environmental variables, to perform a Partial CCA, controlling for the spatial structure, in order to retain only the most parsimonious factors from all sets of predictors, even though some of them may have been ignored in the global approach. This is called the *additive approach* (Figure 2.4).

Results

GLOBAL APPROACH

Among the dependent zooplankton species assemblage, the most ubiquitous species were *Keratella cochlearis, Kellicottia longispina*, *Bosmina longirostris* and *Polyarthra vulgaris*, and many species were present in more than 66% of the lakes (Appendix 2). The zooplankton density ranged from 7720 to 240 243 ind. m^{-3} among lakes, and increase in zooplankton abundance was related to the longitudinal (east to west) geographical axis (Pinel-Alloul, Méthot & Codin-Blumer, 1987). Preliminary study indicated that zooplankton communities in Québec lakes can be classified into eight different species associations, which were related with the opposite natural acidity and sulphate-alkalinity geographic gradients (Pinel-Alloul *et al.*, 1990a).

The results of the global approach confirm the multiple forces hypothesis. The CCA and Partial CCA applied to all environmental factors (physical and chemical variables, lake morphometry, phytoplankton and fish community structure), controlling for the spatial structure, indicate that both abiotic and biotic factors significantly influence the zooplankton community structure ($P \leq 0.05$, Table II). After the forward selection procedure on the spatial and environmental matrices, 5 spatial factors and 12 environmental factors are retained in the global model. Only 3 chemical variables are selected (Ca^{++}, SO_4^{--}, Mg^{++}), and they represent one of the major features in water chemistry associated with the hardness-alkalinity and sulphate gradients. No morphometric factor is retained in the global approach. The phytoplankton composition is related to the zooplankton community structure; the most discriminant taxa are cyanophytes (*Merismopedia minima*, *Microcystis* sp.), chlorophytes (*Gloeocystis* sp., *Cosmarium* sp.) and chrysophytes (*Desmerella* sp., *Dinobryon crenulatum*). Fish community composition also influences the zooplankton assemblages, which vary significantly according to the importance of yellow perch (*Perca flavescens*) and piscivorous fish as walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*).

TABLE II. Variance explained by each spatial and environmental factors retained after forward selection in the CCA and partial CCA based on all environmental factors (global approach)

Type of environmental factors	Variable	Variance explained (%)	Significance *P*-value
Spatial	x	0.10	0.01^{**}
	y	0.07	0.01^{**}
	x^2	0.04	0.01^{**}
	x^2y	0.04	0.03^{*}
	y^3	0.04	0.01^{**}
Physical and chemical	Ca^{++}	0.11	0.01^{**}
	SO^{4-}	0.06	0.01^{**}
	Mg^{++}	0.03	0.02^{*}
Phytoplankton	*Merismopedia minima*	0.05	0.01^{**}
	Cosmarium sp.	0.04	0.03^{*}
	Microcystis sp.	0.03	0.03^{*}
	Gloeocystis sp.	0.03	0.03^{*}
	Desmerella sp.	0.03	0.03^{*}
	Dynobrion crenulatum	0.03	0.04^{*}
Fish	*Perca flavescens*	0.08	0.01^{**}
	Stizostedion vitreum	0.06	0.01^{**}
	Esox lucius	0.04	0.02^{*}

** $P \leq 0.01$; * $P \leq 0.05$.

Figure 3 (stacked histogram G.A.) illustrates the relative importance of the pure environmental fraction (a), the spatially-structured environmental fraction (b), the pure spatial fraction (c) and the undetermined fraction (d) of the zooplankton variation according to the global approach. The total environmental contribution (fraction a+b: 45.2%) is significant ($P = 0.01$). The pure contribution of the 12 environmental variables (fraction a) is large (30.4%) and significant ($P = 0.01$) while the purely spatial contribution (fraction c) is low (8.0%) and not significant ($P = 0.12$). Comparing fraction (a) to (a + b) indicates that the effect of the environmental variables on the zooplankton remains the same to a large extent [30.4/(30.4+14.8) = 67%], independently of the geographic positions of the lakes. The fact that the pure spatial fraction (c) is not significant indicates that most of the among-lake zooplankton spatial variation (8.0 + 14.8 = 22.8%) has been explained by the spatially structured environmental factors related to geographic gradients in water chemistry, phytoplankton and fish community structure.

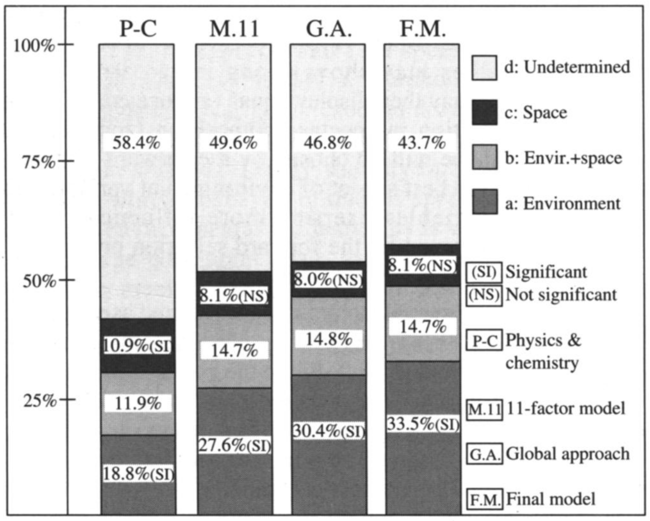


FIGURE 3. Variation partitioning of the zooplankton data matrix according to different models. P-C: independent approach using the physical and chemical environmental factor set; M.11: additive approach using the 11 most parcimonious environmental factors (see Table VI); G.A.: global approach using the 12 selected environmental factors (see Table II); F.M.: final model retained in the additive approach considering the 16 environmental factors selected by the independent approaches.

However, the large amount of unexplained variation (d: 46.8%) suggests that other external factors (intra-lake spatial heterogeneity, local abiotic and biotic factors, community dynamics), not taken into account in the study, can exert some influence on zooplankton composition variation.

INDEPENDENT APPROACHES

Here, we analyse independently the effects of each set of environmental variables, controlling for the spatial structure. Due to differences in collinearity among independent variables, the forward selection procedure (Table III) separately applied to each set of explanatory variables does not retain exactly the same environmental factors as the global approach based on all environmental factor sets. Among the abiotic factors, four other physical and chemical variables are added while three lake morphometry variables (morphoedaphic index, mean depth and altitude) are also retained. The selected physical and chemical variables can be classified into two opposite categories: those related to the hardness-alkalinity and sulphate factors (Ca^{++}, Mg^{++}, pH, SO_4^{--}) and those related to the water transparency, natural acidity and metal contamination (total Al, Mn^{++}, water transparency). For the biotic factors, the independent approaches delete most of the phytoplankton taxa and fish species retained by the global approach while adding new variables. Two of the phytoplankton taxa (*Merismopedia minima*, *Cosmarium* sp.) already selected by the global approach are retained again while a new chrysophyte taxon *Kephyrion* is selected. For the fish community, the independent approach selects again two contrasting communities resulting in different zooplankton structures: fish communities dominated by the yellow perch (*Perca flavescens*), on the one hand, and fish communities composed of populations of brook trout (*Salvelinus fontinalis*) and/or castotomids (*Catostomus commersoni*) on the other.

TABLE III. Variance explained by the spatial and environmental factors retained after forward selection in the CCA and partial CCA based on each set of environmental factors (independent approaches)

Type of environmental factors	Variable	Variance explained (%)	Significance *P*-value
Spatial	x	0.10	0.01**
	y	0.07	0.01**
	x^2	0.04	0.01**
	x^2y	0.04	0.03*
	y^3	0.04	0.01**
Physical and chemical	Ca^{++}	0.11	0.01**
	SO$_4^{--}$	0.06	0.01**
	Mg^{++}	0.06	0.01**
	Mn^{++}	0.05	0.01**
	pH	0.04	0.01**
	Total Al	0.04	0.01**
	Transparency	0.04	0.01**
Morphometry	Altitude	0.07	0.01**
	Mean Depth	0.05	0.02*
	Morphoedaphic index	0.04	0.03*
Phytoplankton	*Merismopedia minima*	0.06	0.04*
	Kephyrion sp.	0.05	0.04*
	Cosmarium sp.	0.04	0.04*
Fish	*Perca flavescens*	0.09	0.01**
	Salvelinus fontinalis	0.06	0.01**
	Catostomus commersoni	0.05	0.01**

**: $P \leq 0.01$; *: $P \leq 0.05$.

Figure 4 illustrates the relative importance of the pure environmental fraction (a), the spatially-structured environmental fraction (b), the pure spatial fraction (c) and the undetermined fraction of the zooplankton variance for each set of environmental factors. The total physical and chemical contribution (fractions a + b: 30.7%) is more important than that of the total phytoplankton (11.2%) and fish (15.6%) community contributions, confirming the second hypothesis on the primacy of the abiotic factors in explaining the large-scale geographical variation in zooplankton community structure within Québec lakes. The pure effect of the morphometric factors is not significant (5.2%; $P = 0.35$).

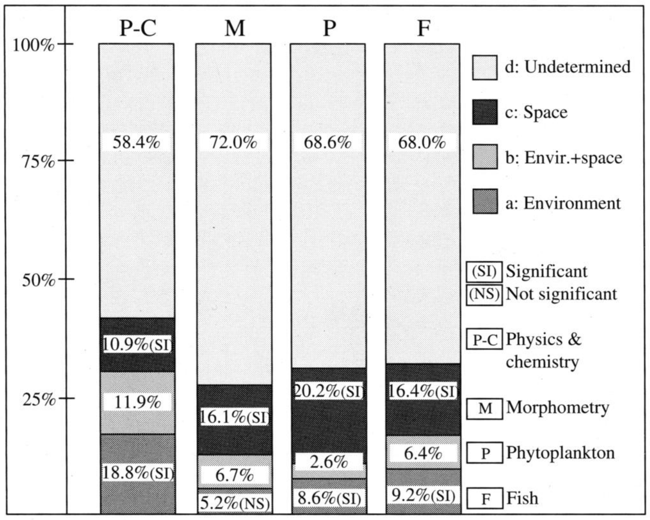


FIGURE 4. Variation partitioning of the zooplankton data matrix according to the independent approaches. P-C: model using the physical and chemical environmental factor set; M: model using the morphometric environmental factor set; P: model using the phytoplankton factor set; F: model using the fish factor set.

Contrary to the results obtained with the global approach, the purely spatial contributions (c) to zooplankton composition variation are significant for each set of variables, ranging from 10.9 to 20.2%, which indicates that each set of variables is not capable of explaining alone the spatial variation of lake zooplankton in Québec lakes. The unexplained fractions (d) remain high (58 to 72%) in all four cases.

The CCA results for each explanatory set can be displayed in the form of species-environment ordination biplots where environmental variables are depicted by arrows and zooplankton species are marked by points (Figure 5). Only the environmental factors retained in each model by the forward selection procedure are presented. These species-environment biplots allow us to infer the zooplankton species responses to the main environmental gradients, according to the approximate value of their abundance weighted average with respect to the specific environmental variables retained in the model (ter Braak, 1987). For the physical and chemical factors (Figure 5a), canonical axis I (17.6%) and axis II (12.2%) explain a significant amount of the variance in the species-environment biplot. In the ordination diagram, the lengths of the total Al, Ca^{++}, pH, Mg^{++} and SO$_4^{--}$ arrows along CCA axis I clearly indicate that these chemical variables are the most important to explain water chemistry variation among lakes. The position of the Al and Ca^{++} arrows shows that they are inversely related. Ca^{++} with positive loading on axis I represents the hardness-alkalinity gradient and is strongly related to the sulphate gradient. Inversely, Al with negative loading on axis I indicates the acidity and metal contamination gradient. Arrows of Mn^{++} and water transparency (TR) are shorter and follow CCA axis II with positive loadings. Because Ca^{++} and Al are the most important variables representing the two opposite physical and chemical gradients among lakes, we examine their influence on zooplankton species distribution. Table IV presents the zooplankton taxa scores when the CCA ordinations have been constrained to be linear combinations of either the Ca^{++} or the Al environmental axes. Positioning of zooplankton taxa along the Ca^{++} axis provides strong evidence that the rotifers *Filinia longiseta* (FILO), *Keratella quadrata* (KEQU) and *Synchaeta* (SYNC), the cladocerans *Diaphanosoma* sp. (DIAH), *Daphnia galeata mendotae* (DAGA), *Sida crystallina* (SICR) and *Ceriodaphnia reticulata* (CERE), and the copepods *Tropocyclops prasinus* (TRPR), *Mesocyclops edax* (MEED), *Skistodiaptomus oregonensis* (SKOR), *Diacyclops bicuspidatus thomasi* (DIBT) and *Leptodiaptomus sicilis* (LESI) predominate in more alkaline lakes. In opposite, the positions of the taxa along the Al axis indicate that the rotifers *Keratella taurocephala* (KETA), *Keratella hiemalis* (KEHI) and *Gastropus* (GAST), the cladocerans *Daphnia rosea* (DARO), *Daphnia schloderi* (DASC) and *D. longiremis* (DALO), and the copepods *Leptodiaptomus ashlandi* (LEAS) and *Cyclops scutifer* (CYSC) occur in the most acidic and metal contaminated waters. Otherwise, the rotifers *Conochilus unicornis* (COCO), the cladocerans *Holopedium gibberum* (HOGI), *Leptodora kindtii* (LEKI) and *Daphnia dubia* (DADU), and the calanid *Leptodiaptomus minutus* (LEMI) are characteristic of lightly acidic waters. The other zooplankton taxa share ubiquitous positions and occur in circumneutral lakes. For the morphometric factors

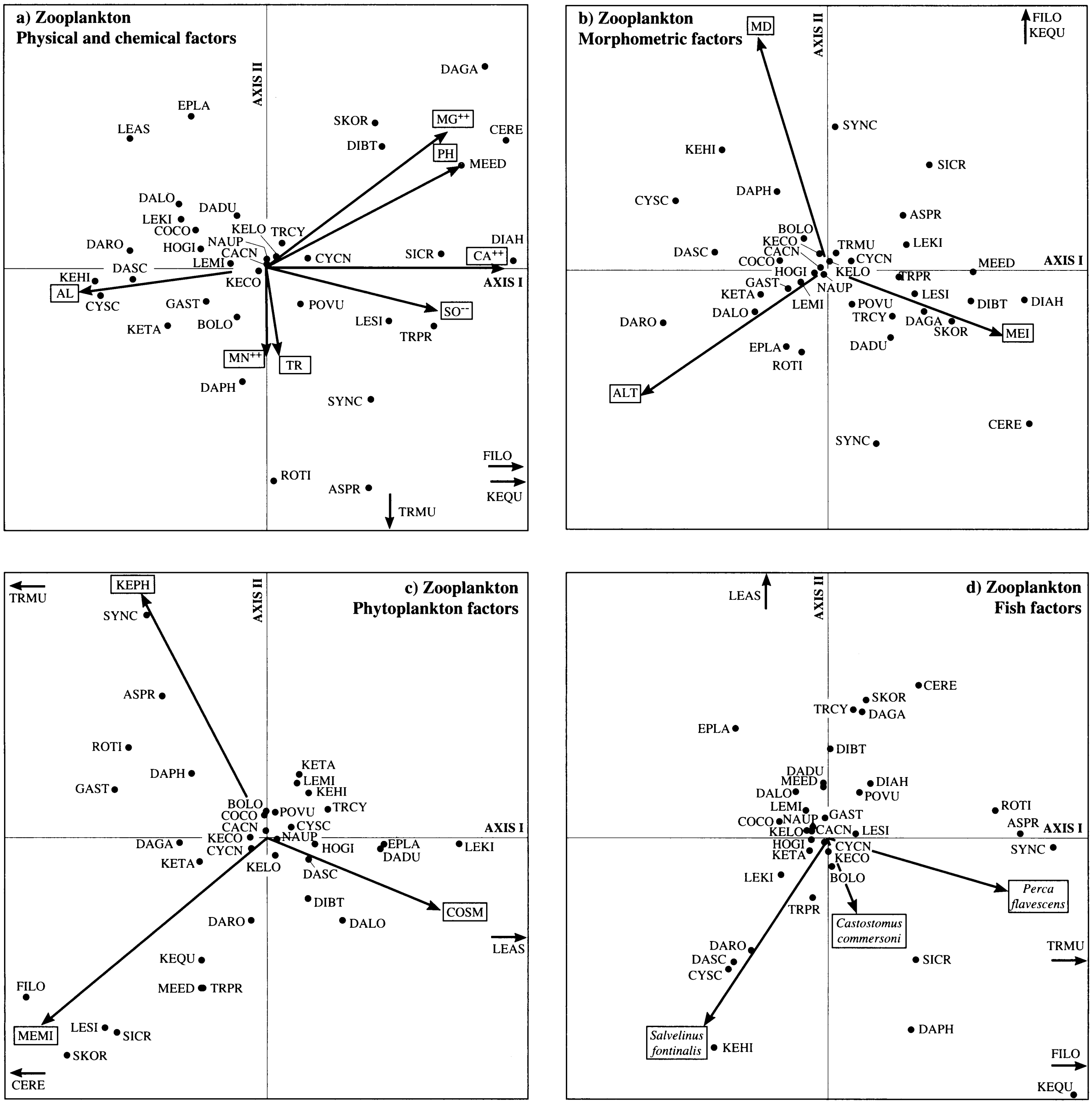


Figure 5. Canonical correspondence analysis (CCA) ordination biplots of each set of environmental factors and zooplankton species. A: zooplankton - physical and chemical factors; B: zooplankton - morphometric factors; C: zooplankton - phytoplankton factors; D: zooplankton -fish factors. Only the environmental factors retained in each independent model by the forward selection procedure are presented. For zooplankton taxa codes, see Table IV.

(Figure 5b), CCA axes I and II explain 27.8% and 18.8% respectively of the variance in the species-environment biplot. Along axis I, the morphoedaphic index (MEI) and altitude (ALT) are the most important variables and are inversely related. These variables represent the trophic gradient with high MEI in southwestern lakes of low altitude. The mean lake depth variable (MD) has highly positive loading along axis II and indicates the lake depth and water transparency factor. Positioning of zooplankton taxa along the MEI-eutrophy axis provides strong evidence that most of the species previously associated with alkaline waters have high loadings on this axis, whereas some species *Keratella hiemalis* (KEHI), *Synchaeta* sp. (SYNC) and the cyclopid *Cyclops scutifer* (CYSC) are associated with deep lakes. For the phytoplankton factors (Figure 5c), CCA axes I and II explain 20.2% and 16.6% of the variance in the zooplankton-phytoplankton biplot, respectively. The chlorophyte *Cosmarium* sp. (COSM) and the cyanophyte *Merismopedia minima* (MEMI) are inversely related along the axis I while the chrysophyte *Kephyrion* sp. (KEPH) is positively associated to axis II. The fact that a large proportion of the zooplankton species display central positions in

TABLE IV. Zooplankton taxa scores in the CCA ordination that have been constrained to be linear to the Ca^{++} and Al environmental factors which explain the maximum amount of zooplankton variation. Species codes correspond to those presented in Figure 5

Zooplankton taxa	Codes	Axis Ca^{++}	Axis Al
Rotifera			
Filinia longiseta	FILO	2.3569	- 1.2303
Keratella quadrata	KEQU	1.7302	- 0.7809
Synchaeta sp.	SYNC	0.6153	- 0.3920
Asplanchna priodonta	ASPR	0.2714	- 0.1608
Trichocerca multicrenis	TRMU	0.1856	- 0.1867
Polyarthra vulgaris	POVU	0.0866	- 0.0714
Kellicottia longispina	KELO	0.0596	- 0.0315
Keratella cochlearis	KECO	- 0.0080	- 0.0050
Trichocerca cylindrica	TRCY	- 0.0532	- 0.0946
Conochilus unicornis	COCO	- 0.2714	0.1403
Gastropus sp.	GAST	- 0.2838	0.2256
Keratella hiemalis	KEHI	- 0.3258	0.2641
Keratella taurocephala	KETA	- 0.4239	0.2875
Undetermined Rotifera	ROTI	- 0.4460	0.0675
Cladocera			
Diaphanosoma sp.	DIAH	0.7238	- 0.7850
Daphnia galeata mendotae	DAGA	0.6968	- 0.7152
Sida crystallina	SICR	0.4029	- 0.9602
Ceriodaphnia reticulata	CERE	0.2448	- 0.0945
Daphnia sp.	DAPH	- 0.0735	0.1186
Bosmina longirostris	BOLO	- 0.0750	0.0652
Daphnia dubia	DADU	- 0.1933	- 0.0869
Leptodora kindtii	LEKI	- 0.2093	- 0.0265
Holopedium gibberum	HOGI	- 0.2552	0.1297
Daphnia rosea	DARO	- 0.3021	0.8101
Daphnia schloderi	DASC	- 0.3320	0.4312
Daphnia longiremis	DALO	- 0.3476	0.2150
Copepoda Calanoida			
Skistodiaptomus oregonensis	SKOR	0.5439	0.1236
Leptodiaptomus sicilis	LESI	0.3250	- 0.2240
Copepodid calanoïds	CACN	0.0280	0.0044
Leptodiaptomus minutus	LEMI	- 0.1287	0.0674
Epischura lacustris	EPLA	- 0.1748	0.2636
Leptodiaptomus ashlandi	LEAS	- 0.4051	0.6978
Copepoda cyclopoida			
Tropocyclops prasinus mexicanus	TRPR	0.6436	- 0.0663
Mesocyclops edax	MEED	0.6315	- 0.5697
Diacyclops bicuspidatus thomasi	DIBT	0.3378	- 0.3106
Copepodid cyclopoids	CYCN	0.1539	- 0.1806
Cyclops scutifer	CYSC	- 0.2988	0.5855
Nauplii	NAUP	0.0293	- 0.0070

the ordination diagram (Figure 5c) indicates that the zooplankton-phytoplankton relationships are not as strong as those observed with the chemical factors. However, some co-occurrences and associations between zooplankton and phytoplankton taxa can be discerned. The rotifer *Filinia longiseta* (FILO), the cladocerans *Sida crystallina* (SICR) and *Ceriodaphnia reticulata* (CERE) as well as two copepods (*Leptodiaptomus sicilis* (LESI), *Skistodiaptomus oregonensis* (SKOR)) are strongly associated to the cyanophyte *Merismopedia minima* (MEMI) while the rotifers *Synchaeta* sp. (SYNC) and *Asplanchna priodonta* (ASPR) are linked to the chrysophyte taxa *Kephyrion* (KEPH). Finally, large calanids and cladocerans (*Epischura lacustris* (EPLA), *Leptodiaptomus ashlandi* (LEAS), *Leptodora kindtii* (LEKI)) are related to the chlorophyte taxon *Cosmarium* sp. (COSM). Based on fish, CCA axis I (40.6%) and axis II (28.9%) explain a large amount of the variance in the species-environment biplot (Figure 5d). Axis I is positively related to high abundances of yellow perch (*Perca flavescens*) while axis II is negatively associated with fish community dominated either by allopatric populations of *Salvelinus fontinalis* (11/54 lakes) or by sympatric populations of *Salvelinus fontinalis* and *Catostomus commersoni* (10/54 lakes). Rotifer dominance (*Keratella quadrata* (KEQU), *Filinia longiseta* (FILO), *Tricocherca multicrenis* (TRMU), *Synchaeta* sp. (SYNC), *Asplanchna priodonta* (ASPR)) is associated with high abundances of yellow perch. The cyclopid *Cyclops scutifer* (CYSC), the daphnids (*Daphnia schlodleri* (DASC), D. *rosea* (DARO)), and the rotifer *Keratella hiemalis* (KEHI) occur mainly in association with salmonid fish communities, and inversely for large crustaceans (*Skistodiaptomus oregonensis* (SKOR), *Ceriodaphnia reticulata* (CERE), *Daphnia galeata mendotae* (DAGA)) which are associated to lakes containing piscivorous fish.

DIFFERENTIAL APPROACHES

In order to determine the relative importance of different sets of environmental factors, we adopted a differential approach and applied Partial CCA to a combination of sets of factors (Table V) without taking the spatial structuring into account. The variance partition of the zooplankton community was computed with the CCA procedure, partialling out the first set or combination of sets of environmental

TABLE V. Variance partition of the zooplankton community by a combination of sets of factors. The value of ∂R^2 represents the effect on R^2 (percentage of variation explained by the two sets of factors) of adding the second set of variables; the P-value is computed with the CCA procedure, partialling out the first set of variables from the analysis and looking at the significance that remains for the second set (differential approaches)

Sets of variables	R^2	∂R^2	P-value
(Physical and chemical) and morphometry	40.0%	4.3%	0.71^{NS}
(Physical and chemical) and phytoplankton	36.9%	6.2%	0.02^{*}
(Physical and chemical) and fish	39.1%	8.5%	0.01^{**}
(Physical and chemical, phytoplankton) and morphometry	41.5%	3.8%	0.82^{NS}
(Physical and chemical, phytoplankton) and fish	45.2%	7.5%	0.01^{**}
(Physical and chemical, fish) and morphometry	42.0%	2.9%	1.00^{NS}
(Physical and chemical, fish) and phytoplankton	45.2%	6.1%	0.02^{*}
(Phytoplankton, fish) and morphometry	30.9%	6.8%	0.03^{*}
(Phytoplankton, fish) and (physical and chemical)	45.2%	21.1%	0.01^{**}
(Morphometry, phytoplankton, fish) and (physical and chemical)	48.2%	17.4%	0.01^{*}
(Physical and chemical, phytoplankton, fish) and morphometry	48.2%	3.0%	0.96^{NS}

** $P \leq 0.01$; * $P \leq 0.05$; NS: $P > 0.05$.

variables from the analysis and looking at the significance that remains for the second set. Our results show that the highest amounts of explained zooplankton variation (45.2 to 48.2%) were obtained with three sets of factors (physical and chemical, phytoplankton, fish) or all four sets (+ morphometry). The importance of the physics and chemistry is well demonstrated since taken alone, this set of factors explains 30.7% of the total zooplankton variation (Figure 4), while in combination with other sets of factors it explains a significant additional amount of variation (17.4 to 21.1%, Table V). The morphometric factors did not add a significant amount of explained variation when used as a second set of variables for the physical and chemical factors alone, or for combinations of sets of environmental factors, including the physical and chemical ones. Lake morphometry contribution is significant only when added to the set of biotic factors (phytoplankton and fish). On the contrary, the phytoplankton and fish variables always add a significant amount of explained variation to the amount of variance explained by the physical and chemical factors alone or by a set of abiotic and biotic variables.

ADDITIVE APPROACH: SPATIAL AND ENVIRONMENTAL COMPONENTS OF FRESHWATER ZOOPLANKTON STRUCTURE

To determine the most parcimonious set of environmental components of freshwater zooplankton variation, we performed CCA and Partial CCA analyses, controlling for space, including as environmental factors only those retained by forward selection from all sets of environmental variables when analyzed independently. Prior to the CCA analysis, forward selection procedure was used again to choose among the 16 environmental factors of Table III, those which remain significant (Table VI). Eleven factors (6 chemical variables: Ca^{++}, SO_4^{--}, Mg^{++}, Mn^{++}, pH, Al; 2 phytoplankton taxa: *Merismopedia minima*, *Cosmarium* sp.; 3 fish species: *Perca flavescens*, *Salvelinus fontinalis*, *Catostomus commersoni*), remain significant while all morphometric variables, water transparency, and the chrysophyte species *Kephyrion* sp. are eliminated. This again indicates that the morphometric variables add nothing to the explained variance of the zooplankton data; they seem spatially related to the physical and chemical gradients.

TABLE VI. Variance explained by each selected factor among the 16 environmental factors retained for each set (additive approach)

Type of environmental factors	Variable	Variance explained (%)	Significance *P*-value
Spatial	x	0.10	0.01**
	y	0.07	0.01**
	x^2	0.04	0.01**
	x^2y	0.04	0.03*
	y^3	0.04	0.01**
Physical and chemical	Ca^{++}	0.11	0.01**
	SO_4^{--}	0.06	0.01**
	Mg^{++}	0.05	0.01**
	Mn^{++}	0.03	0.02*
	pH	0.03	0.03*
	Al	0.03	0.02*
Phytoplankton	*Merismopedia minima*	0.04	0.02*
	Cosmarium sp.	0.04	0.02*
Fish	*Perca flavescens*	0.08	0.01**
	Salvelinus fontinalis	0.06	0.01**
	Catostomus commersoni	0.03	0.04*

** $P \leq 0.01$; * $P \leq 0.05$.

Comparisons of results (Figure 3) show that both the total amount of explained variation (a + b + c) and the fraction explained by the environmental variables in the model (a + b) increase from the model based solely on the physical and chemical variables (P-C), to the additive approach with 11 environmental factors (M-11), to the global approach results (G.A.), to reach a maximum with the model including the 16 abiotic and biotic factors retained in the independent approaches (F.M.). This comparison also reveals that fractions (c), the unexplained spatial effects, are about the same and not significant for the M.11, G.A., and F.M. models. Increasing the number of significant environmental variables from 11 (M.11) in the additive model to 16 (F.M.) in the final model results in reducing the undetermined fraction (d: 49.6 to 43.7%) and increasing the non-spatially environmental fraction (a: 27.6 to 33.5%). In all three models including abiotic and biotic factors, the covariation (b) is equally important (14.7-14.8%). The undetermined fractions of variance are high enough (43.7 to 49.6%) to indicate that other sources of variation are present. The best final model (F.M.) which is the one with the lowest unexplained variance, takes into consideration the contribution, significant or not, of each set of predictors and seems more realistic than the model obtained by the global approach, since it includes all features of the environmental heterogeneity such as water chemistry and transparency, lake morphometry and phytoplankton and fish community structure that are generally recognized as important. The more parcimonious model with 11 factors is less interesting in terms of explanation since it gives supremacy to only two of the most important gradients across the spatial environmental heterogeneity of Québec lakes: the oriented northeast-to-southwest hardness-alkalinity and suphate gradients, leaving little strength to the opposite oligotrophy-acidity gradient, which is reflected only by one chemical factor (metal contamination by Al) and one indicator fish species (*Salvelinus fontinalis*).

The zooplankton community structure, as explained by the environmental variables retained in the final model (F.M.), is mapped in Figure 6. Figure 6a clearly shows that the total environmental explained variation (fractions a + b) along axis I is largely spatial. There is a geographic gradient in the zooplankton structure, with an increase in the first canonical axis values oriented northeast (Havre-St-Pierre, Sept-Iles and Manicouagan) to southwest (Maniwaki, La Tuque and Chapais); the orientation of this figure is such that the "lower" values on canonical axis I are down front, not hidden by the "higher" values located upward. Since the first canonical axis is positively related to Ca^{++}, Mg^{++}, SO_4^{--}, pH (0.53 to 0.76), MEI (0.44), *Merismopedia minima* (0.40) and yellow perch (0.47), and negatively related to Al (- 0.66), altitude (- 0.58) and brook trout (- 0.53), this general trend illustrates the zooplankton community response to the inversed hardness-eutrophy-planktivory and acid-metal-piscivory environmental gradients. Local variations opposite to this general northeast-to-southwest trend occur in some lakes (lake 224B in La Tuque) and in most

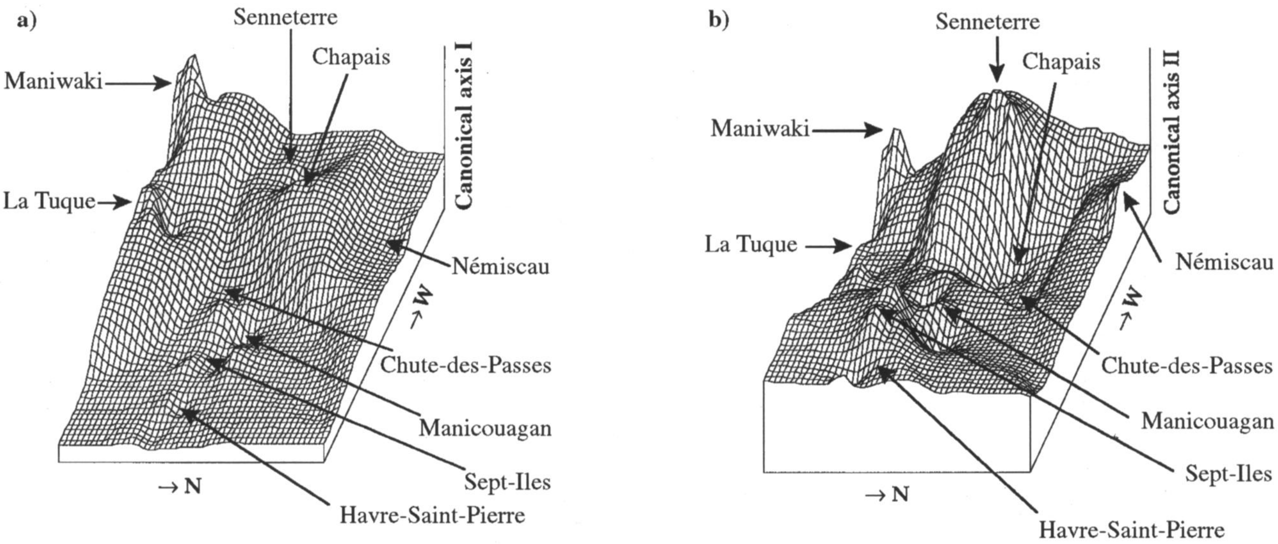


Figure 6. Maps of the canonical axes of the total environmental fraction of the zooplankton variation (fractions a + b) based on the final model comprising 16 environmental factors (see Table III). A: first canonical axis; B: second canonical axis. The orientation of the figures are north-east (right downward corner) to south-west (left upward corner) in such a way that the lower values on canonical axes are down front and not hidden by the higher values located upward. Arrows indicate the geographical areas from Figure 1.

lakes in the Senneterre and Nemiscau areas. On the second axis (Figure 6b), we illustrate the acidification gradient where positive loadings are associated to yellow perch dominance (0.64), the acidic taxa *Kephyrion* (0.50), greater mean depth and water transparency (0.29 and 0.21), and higher water concentrations in Al and Mn^{++} (0.15 and 0.23). It becomes obvious, from the bumpy feature of the map of the total environmental-explained variation along axis II, that there is no continuous geographic gradient in lake acidity in relation to zooplankton community structure across Québec. The most acidified lakes are located in the Maniwaki (lake 147C) and Senneterre areas. Some lakes in Manicouagan (lake 59A), Sept-Iles (lakes 30A and 30B) and Havre-St-Pierre (lake 22C) as well as lake 188 in Nemiscau are also acidic. In contrast, lakes located in the Chapais and Chute-des-Passes areas are the less acidic. This dual presentation of the total environmental-explained variance in zooplankton structure along canonical axes reveals that most of the spatially-structured environmental variation (fraction b: 14.7%) is caused by the hardness-alkalinity geographic gradient while the non-spatial environmental variation (fraction a: 33.5%) is accounted for by the regional variation in acidity and metal contamination, phytoplankton and fish community structures.

Discussion

SUPPORT FOR THE MULTIPLE FORCES HYPOTHESIS

Both the global, differential and additive approaches support the multiple forces hypothesis and show that the control model of the zooplankton structure within Québec lakes includes both abiotic factors (mainly related to the water chemistry gradients) and biotic bottom-up (phytoplankton) and top-down (fish) factors. The best final model can explain nearly half (48.2%) of the total variance in zooplankton species assemblages. When considering only one set of abiotic or biotic factors at a time, as in the independent approaches, their total contribution, when significant, explains only 11.2 to 30.7% of the zooplankton structure variability among lakes. Thus, consideration of both sets of factors (abiotic and biotic) in concert has proven to substantially increase our ability to predict changes in zooplankton species composition. As stated by Carpenter & Kitchell (1992), "if variance explained by trophic interactions or top-down fish effect adds to variation explained by abiotic factors or nutrient load, then we can build on the foundation that the trophic cascade argument attempts to place food-web interactions in the context of the multiple physical and chemical factors that govern lake dynamics". Our study clearly confirms this statement and indicates that neither the abiotic model, mostly based on close correlates of nutrients (conductivity, alkalinity), nor the top-down trophic cascade model, fully perform as single-factor environmental models. These models are complementary and not contradictory. Earlier studies attempting to estimate the simple and combined effects of bottom-up and top-down forces are few in number. In enclosure experiments, Mazumder *et al.*, (1988) tested the multiple driving forces hypothesis on limnoplankton size spectra, as expressed by the size distribution of particulate phosphorus (PP); they demonstrated that both fertilization and the addition of planktivorous fish affected the nanoplankton (2-20 μm) and the mesoplankton (> 200 μm) fractions, the fish effect having primacy. The only *in situ* comparative study assessing the effects of abiotic and biotic factors on the zooplankton structure was recently conducted on 43 Laurentian Shield lakes (Rodriguez, Magnan & Lacasse, 1993) at small regional scale, and only considered cladoceran species assemblages. Again, the results of this study support the multiple forces hypothesis and showed that both abiotic factors (maximum depth, conductivity) and fish community composition influenced cladoceran taxa distribution, but, contrary to our results, few abiotic variables entered their final models. The limited predictive power of most of the abiotic variables may be partly due to the regional nature of their study, because natural variation in physical and chemical variables was relatively small over their small sampling area. This opposition between the results of these two *in situ* studies (Rodriguez, Magnan & Lacasse, 1993; present study), which differ by their sampling scales, lead to develop alternative hypotheses to explain the effect of scaling on the relative roles of driving abiotic and biotic forces in environmental control models. We could hypothesize that over a large geographic scale, abiotic forces should be predominant and that, in constrast, the biotic forces should have the primacy at small regional scale. Indeed, spatial heterogeneity in community composition and the analysis of its relation to habitat heterogeneity are scale-dependent (Hoekstra, Allen & Flather, 1991). In a conceptual framework of the effect of scaling on processes structuring community composition, one views the structuring factors, events and processes as a series of filters acting on the communities at continental, regional, lake-type, and local scales to produce different patterns of community composition or species distribution (Tonn *et al.*, 1990). We already analysed within-lake patterns of zooplankton distribution at fine to macro-scales (Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991). The present study can thus be placed within this framework as an additional filter of among-lake factors which acts on zooplankton community to produce large-scale geographic heterogeneity in community composition.

Spatial polynomials of the geographical coordinates, as used in this study, are efficient in modeling large-scale variability in the biological data, when taken alone (22.8%: see statistical analyses in Methods) or taken in combination with only one set of environmental factors (Figure 4). However, the non-significant spatial fractions of variation (c) in our M.11, G.A., and F.M. models indicate that most of the among-lake zooplankton variation has been explained by the spatially-structured environmental factors related to gradients in water-chemistry, fish and phytoplankton community structure included in the analysis. Thus, it is likely that no other important, large-scale spatial structuring process has been missed within the geographical scale of our study. This means also that the large fractions (c) and (d) of zooplankton variation uncovered by our analyses are not regional (i.e., large-scale) in nature, but the result of local processes that remain unexplained for the time being.

PRIMACY OF THE ABIOTIC ENVIRONMENTAL CONTROL MODEL

Discussing the processes that are likely to structure aquatic ecosystems, Allen & Star (1982) and Amanieu *et al.*, (1989) present an argument founded on hierarchy theory. They remind us that physical processes *sensu lato* constitute the first step of the hierarchy of processes controlling ecosystems and influencing biological sub-systems while, conversely, physical processes are little influenced by biological systems. The physical processes acting upon the physics and chemistry of the lakes under study are mostly geomorphological and geological (hardness-alkalinity, acidity and metal contamination) on the one hand, and climatic (including wind dispersion of pollutants and sulfate deposition by acid precipitation), on the other; both types are likely to generate large-scale spatial structures among the lake physical and chemical conditions. This is supported by our results, which show (Table III; Figures 4 and 6) that the chemical variables have a greater contribution to the zooplankton explained variance than the small-scale physical processes (as measured by the morphometric variables) or the biotic control variables (phytoplankton and fish). However, with only a maximum of 56.3% of variance explained in our final model, it is difficult to conclude that abiotic factors are the more important forces explaining large-scale zooplankton heterogenity. Both abiotic and biotic factors can account for much of the unexplained variance. Despites the great number of abiotic factors accounted in the study, some important variables (particulate organic carbon, total nitrogen and phosphorus, mixed layer depth, wind exposure) were not measured; they could influence among-lake and within lake variability. Biotic factors related to food web interactions (competition, resource quality, community dynamics, behaviour, components of the microbial loop) are not measured at all and also might account for zooplankton heterogeneity. In future studies of this type it would also be preferable to used metered nets and a range of net sizes and sampling protocols to quantify with equal efficiency the diverse size components of the micro and macrozooplankton.

However, considering only the abiotic forces and the explained variance, the geographic inverse gradients of alkalinity, hardness and sulphate from northeast to southwest, and that of acidity and metal contamination from southwest to northeast are the major features in water chemistry influencing zooplankton community composition. A predominant effect of water hardness on composition and size-structure of zooplankton communities was also detected by Tessier & Horwitz (1990) in 146 lakes in northeastern United States, large zooplankton becoming scarce in softwaters. A recognition that water chemistry can have primacy on structuring zooplankton community by restricting proliferation of large-bodied zooplankton has important implications to zooplankton community ecology and lake management because these large zooplankters are key components of the planktonic food web. They are the most general and efficient grazers, and thus sustain the flux of carbon through higher trophic levels. Thus, if large zooplankton are excluded from softwater lakes, these lakes are less productive and more sensitive to global and anthropogenic changes in bottom-up abiotic forces. In corollary, these lakes may be unable to respond to biomanipulation management and variation in planktivory as the more hardwater lakes do.

COMPLEMENTARITY OF THE BIOTIC CONTROL MODEL

Both phytoplankton and fish community structures are complementary processes in locally structuring zooplankton assemblages within Québec lakes, but their strengths are less than half that of water chemistry. The total contribution of phytoplankton and fish community to the zooplankton composition variance are 11.2 and 15.6%, respectively, compared to 30.7% for the physical and chemical variables. Furthermore, the fish effect is always more important in terms of variance contribution than the phytoplankton effect, either in the independent or the differential approaches. The complexity of interactions between fish, zooplankton and algae has been demonstrated by enclosure experiments (Vanni & Findlay, 1990; Turner & Mittelbach,

1992) and biomanipulation studies (Carpenter & Kitchell, 1992). The presence of planktivorous fish not only influences zooplankton community structure, but can have direct (phosphorus recycling) and indirect (lower grazing rate, higher phosphorus regeneration by small-bodied zooplankters) effects on phytoplankton abundance and composition. In enclosures and lakes containing planktivorous fish, phytoplankton biomass was higher and green and blue-green algae more abundant than in enclosures and lakes lacking planktivorous fish where, in contrast, biomass was low and chrysophytes more abundant. However, the phytoplankton-zooplankton link acts as a bottleneck in the trophic cascade model and dampens the planktivory effect on low trophic levels (McQueen & Post, 1988). Whole-lake experiments and long-term records indicate that piscivory would have to change by at least an order of magnitude before statistically reliable changes in phytoplankton could be observed, and that cascading of planktivory is more often observed in oligotrophic than in eutrophic ecosystems (McQueen *et al.*, 1992).

Although phytoplankton composition explains only a small fraction (11.2%) of zooplankton variation when used alone (Figure 4), its addition to physical and chemical factors or to the set of abiotic and biotic factors in the CCA models (Table V) always adds a significant amount of explained variance (about 6%). However, one can wonder if phytoplankton-zooplankton relationships result from indirect associations to the same environmental gradients or from direct trophic relationships. Pinel-Alloul *et al.*, (1990b) showed that most of the phytoplankton taxa selected either by the global, independent or additive approaches were related to one or several environmental gradients. The cyanophyte *Microcystis* sp. and the chlorophytes (*Cosmarium* sp., *Gloeocystis* sp.) were positively related either to the hardness-alkalinity or the sulphate factors while the colonial cyanophyte *Merismopedia minima* was negatively associated with the opposite lake depth and transparency factor. Among the selected chrysophytes, species showed opposite trends. The species *Desmerella* sp. was the only one showing a low positive correlation with the hardness-alkalinity and sulphate factors. The other chrysophytes indicated the reverse environmental gradient; *Dinobryon crenulatum* was the species most strongly related to the lake depth and transparency factors, while the chrysophyte *Kephyrion* sp. as well as its covariate species *Mallomonas* were the only species highly inversely related to the hardness-alkalinity factor. The phytoplankton taxa selected in our models also discriminate from each other by their environmental distribution responses. All the cyanophyte and chlorophyte species retained in our global model, except *Merismopedia minima*, are eutrophic indicators (Rosen, 1981) while the chrysophyte taxa (*Kephyrion*, *Dinobryon crenulatum* and the covariate species *Mallomonas*) are indicators of acidity, oligotrophy and water transparency (Earle, Duthie & Scruton, 1986; Findlay & Kasian, 1986; Willen, 1990; Ilmavirta, 1990). Despite these covariations with the abiotic environmental factors, the spatially-structured component (fraction b; Figure 4) of the total phytoplankton contribution to zooplankton variation is as low as 2.6%; thus, it seems that most phytoplankton-zooplankton relationships come from the non-spatially-structured contribution of the phytoplankton community (fraction (a)/fractions (a + b) = [8.6/(8.6 + 2.6)] = 76.8%).

Fish community composition, taken independently, explains 15.6% of the total variation in zooplankton composition, and adds between 7.5 to 8.5% of additional explained variation when included with one or several sets of physical, chemical and phytoplankton variables. The fish species associated to significant changes in zooplankton structure within Québec lakes can be separated into different categories in relation to their geographic distribution among lakes. The yellow perch (*Perca flavescens*) occurs only in southwestern lakes and the piscivorous walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) in the northwestern lakes. *Salvelinus fontinalis* is characteristic of the fish community in eastern lakes, where it forms allopatric or sympatric populations with *Catostomus commersoni* (Pinel-Alloul & Méthot, 1985). These geographic distributions had already been detected by Legendre & Legendre (1984) in a comprehensive biogeographical study of postglacial dispersal of freshwater fishes in the Québec peninsula.

Relationships between fish and zooplankton communities is not surprising since it has been well demonstrated by enclosure and whole-lake experiments, long-term records and critical reviews (Carpenter, Kitchell & Hodgson, 1985; McQueen, Post & Mills, 1986; Mazumder *et al.*, 1988; Carpenter & Kitchell, 1992; DeMelo *et al.*, 1992). However, our study of zooplankton structure in Québec lakes gives one of the first supports for such relationships over a large-scale multilake comparative survey. We demonstrate that zooplankton assemblages vary according to contrasting fish communities and that size-selective planktivory results in zooplankton communities dominated by small species, in lakes containing fishes such as the yellow perch, or sympatric populations of salmonids and catostomids. In corollary, high piscivory by walleye and northern pike results in large-bodied zooplankton communities. Similar trends were noted in a small-scale study, where Rodriguez, Magnan & Lacasse, (1993) demonstrated that cladoceran assemblages were influenced by the fish community composition. They showed that in lakes with sympatric populations of white sucker and brook trout, *Holopedium gibberum* abundance (which can be considered as a surrogate of large *Daphnia* in their lightly acidic lakes) was reduced by 76-81% while bosminid abundance increased four-fold relative to lakes with brook trout only. The addition of the white sucker was associated with marked changes in the abundance and size structure of bosminids and *Holopedium*. The direct influence of the presence of white sucker on *Holopedium* or large cladocerans is by predation both from the small and large individuals. A second potential indirect impact is mediated by competition between brook trout and white sucker. In white sucker lakes, the diet of brook trout shifts drastically from benthic invertebrates to zooplankton, primarily chaoborids, *Holopedium* and large *Daphnia* (Magnan, 1988; Tremblay & Magnan, 1991). The consequences of variations in piscivory on zooplankton community are also well studied in long-term assays (McQueen *et al.*, 1992) where biomass and numbers of large daphnids (> 1 mm) as *D. pulex* and D. *galeata mendotae* increased when piscivorous fish biomass increased, or in studies of the impact of winterkill of piscivorous fish which results in higher planktivory and a shift to small-bodied zooplankton (Hall & Ehlinger, 1989).

UNEXPLAINED VARIATION

The amount of unexplained variation in our final model is fairly high (43.7%), even assuming that part of it is due to nondeterministic fluctuation. A fair amount of this variation could stem from within-lake spatial heterogeneity, local effects of unmeasured abiotic and biotic variables, local community dynamics, species behavior or small-scale temporal and spatial variation.

Our sampling design limited to a unique integrated composite zooplankton sample per lake, because of logistic and time constraints, does not allow us to consider within-lake spatial heterogeneity in our models. However, it is well demonstrated that within-lake zooplankton patchiness occurs over meso-scale patterns (1-100 km) in large lakes, and from fine- and coarse-scale patterns (1-100 m) to micro-scale patterns (1-100 cm) in smaller lakes, and that it varies with several factors related to density and size of species, volume, depth and scale of sampling (Downing, Perusse & Frenette, 1987; Pinel-Alloul *et al.*, 1988; Pinel-Alloul & Pont, 1991). Cross-systems comparisons of zooplankton heterogeneity at the replicate sample scale indicate also that zooplankton heterogeneity is unrelated to environment and can be predictable for different levels of taxonomic organization using the mean-variance relationships (s^2/m) with a slope varying from 1.2 to 1.9 (Pace, Findlay & Lints, 1991). Applying to our data the s^2/m model of Pinel-Alloul & Pont (1991) developed in a small Canadian Shield lake for integrated water column sampling,

$$s^2 = 0.587\ m^{1.577} \qquad [2]$$

indicates that in our range of zooplankton abundances (7 720 to 240 243 ind. m^{-3}), within-lake spatial heterogeneity at the replicate sample scale would vary 200 fold among lakes and could thus induce a large amount of unexplained variance in our environmental control models. Another difference which could also contribute to the unexplained variance among lakes is the variation in sampling volume (63-628 L); indeed, Downing, Perusse & Frenette (1987) showed that spatial heterogeneity in zooplankton declined with increasing sample volume, a fact which is also well-known and understood in geostatistical theory (Isaaks & Srivastava, 1989: "proportional effect").

Small-scale local effects of abiotic and biotic variables, not taken into account in the present study, may cause spatial heterogeneity in natural populations, and thus add to the amount of unexplained variance in our models. Freshwater zooplankton within-lake heterogeneity is the product of physical processes interacting with many biological and behavioral processes (Pinel-Alloul & Pont, 1991). On the one hand, downwind water currents and Langmuir spirals tend to cause plankton to aggregate in surface waters while vertical Eckman spirals may have a randomizing effect. These aggregation phenomena may depend on the shape and wind exposure of the lake and thus contribute to among-lake zooplankton variability. On the other hand, variation in zooplankton distribution patterns on fine and large scales might also be related to the risk of invertebrate predation, and the ability of a species to compete with other zooplankters (Folt, 1987). Several studies (Vanni, 1988; Lunte & Luecke, 1990) support the hypothesis that invertebrate predation may be a very important determinant of freshwater zooplankton community structure. Chaoborids prey upon small to medium-size zooplankters, and a negative interaction between *Chaoborus* and *Diaphanosoma* distribution patterns has been detected in a small Laurentian Shield lake (Pinel-Alloul & Pont, 1991). However, the effect of invertebrate predation on zooplankton structrure is mediated by vertebrate predation, since in lakes with planktivorous fish, such as sympatric populations of brook trout and white sucker, fish predation on chaoborids decreases the invertebrate predation pressure and could lead to a greater increase in bosminids or small-bodied cladocerans (Rodriguez, Magnan & Lacasse, 1993). Competition between daphnids and rotifers may also account for a fraction of the unexplained variation of zooplankton composition. For instance, the opposition in the ordination biplots between the large *Daphnia galeata mendotae* and most dominant rotifers (*Keratella hiemalis*, K. *taurocephala*, K. *cochlearis*, etc.) reflects competitive exclusion which is improved by reduced fish predation in lakes dominated by walleye and northern pike (Figure 5). Finally, other components of the microbial planktonic loop (autotrophic and heterotrophic picoplankton, heterotrophic nanoplankton), not taken in account in this study, can influence zooplankton structure via grazing interactions (Peterson, Hobbie & Haney, 1978; Knoechel & Holtby, 1986), especially in oligotrophic and humic lakes of the type studied here (Stockner & Shorthreed, 1989; Pinel-Alloul *et al.*, 1989).

IMPLICATIONS FOR SAMPLING DESIGN AND THE DEVELOPMENT OF ENVIRONMENTAL MODELS

Limited success in previous large-scale comparative analyses predicting community composition from a single type of factors prompted a shift of interest toward the experimental approach where one can more clearly detect simple and combined effects of multiple factors using factorial experimental designs. However, generalization of results obtained in laboratory or enclosure studies to complex natural ecosystems is not straightforward, primarily because clear, large-scale patterns against which the experimental results could be compared are lacking (Duarte, Augusti & Canfield, 1992). Our large-scale study provides a clear example to elucidate the dominant mechanisms responsible for the differences in plankton communities across environmental abiotic and biotic gradients, thereby helping to target experimental efforts and fill the gap between experimental and comparative limnology. However, critical aspects of sampling design should be considered and improved to substantially increase the predictive power of the models. As shown by Pinel-Alloul et Pont (1991), within-lake heterogeneity over fine to meso-scale induces a large impredictability. Thus, it is important to replicate sampling within lakes and search for abiotic and biotic variables which vary at this smaller scale to improve zooplankton environmental control models.

In the context of the development of environmental control models based on the ecology of zooplankton communities, our study shows that, when designing zooplankton sampling programs over large spatial scales, we should take into account not only the predominant abiotic factors (nutrients, water-chemistry, lake morphometry) but also the biotic components of zooplankton heterogeneity such as the types of fish community and phytoplankton assemblages. This will substantially increase our capacity to predict zooplankton community, and infer the environmental features of lakes for management and bio-monitoring purposes.

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APPENDIX I. Mean and range of the physical, chemical and morphometric factors used as independent variables in the CCA analyses

Independant variables	Mean	Minimum	Maximum
Morphometric			
Altitude (m)*	362.10	76.00	655.00
Maximum depth (m)*	21.10	4.00	83.00
Mean depth (m)*	5.00	1.20	16.20
Relative depth (%)*	1.40	0.20	4.10
Lake maximal length (km)*	3.40	1.60	7.00
Lake maximal width (km)*	1.20	0.40	2.50
Lake area (ha)*	208.40	36.00	721.00
Watershed area (ha)*	3 855.50	261.00	29 843.00
Lake volume (104 m^3)*	3 741.10	180.00	23 143.00
Lake order*	1.50	1.00	3.00
Lake volume development*	0.80	0.30	2.10
Morphoedaphic index*	7.50	0.60	49.20
Physical and chemical			
Secchi disk transparency (m)*	3.70	1.00	8.00
Color (U. Hazen)*	35.60	5.00	80.00
Conductivity (μS.cm^{-1})*	22.30	6.00	130.00
Hydrogen (H+) (μeq.L^{-1})*	0.90	0.01	5.60
pH*	6.00	5.20	8.30
Alkalinity (μeq.L^{-1})*	107.50	1.00	585.00
Cl (μeq.L^{-1})*	11.80	3.00	25.00
SO$_4$ (μeq.L^{-1})*	76.40	20.80	229.10
Ca (μeq.L^{-1})*	125.60	16.00	678.60
Mg (μeq.L^{-1})*	43.40	6.30	225.30
K (μeq.L^{-1})*	6.60	1.30	14.60
Na (μeq.L^{-1})*	24.30	11.30	46.10
Total Al (μg.L^{-1})*	104.50	14.00	228.00
Mn (μg.L^{-1})*	11.80	1.00	40.00
Fe (μg.L^{-1})*	98.00	14.00	356.00
Zn (μeq.L^{-1})*	6.50	2.00	17.00
DOC (mgL^{-1})*	5.90	2.00	11.00
TOC (mgL^{-1})*	6.10	3.00	11.00
NO$_3$ (μeq.L^{-1})*	0.19	0.08	0.97
Alkalinity/sulphate ratio*	1.26	0.01	8.70

* independent variables retained in the CCA analyses.

APPENDIX II. List and occurrence (No: Number of lakes in which the taxa was recorded) of the zooplankton taxa, phytoplankton taxa and fish species collected in the 54 study lakes. Taxa marked by an asterisk are those retained in the CCA analyses

Zooplankton (No)

Rotifera
_Conochilus unicornis_* (41)
_Kellicottia longispina_* (52)
_Keratella cochlearis_* (53)
_Keratella taurocephala_* (39)
_Keratella quadrata_* (4)
_Keratella hiemalis_* (13)
_Polyarthra vulgaris_* (42)
_Trichocerca cylindrica_* (22)
_Trichocerca multicrenis_* (5)
_Asplanchna priodonta_* (13)
Gastropus sp.* (14)
Synchaeta sp.* (8)
_Filinia longiseta_* (3)
Undetermined Rotifera* (5)
Ploesoma hudsoni (< 3)
Ploesoma sp. (< 3)
Lecane luna (< 3)
Monostyla lunaris (< 3)
Trichotria tetractis (< 3)
Cephalodella gibba (< 3)
Brachionus bidentata (< 3)

Cladocera
_Bosmina longirostris_* (43)
_Holopedium gibberum_* (41)
_Daphnia dubia_* (11)
_Daphnia galeata mendotae_* (14)
_Daphnia schloderi_* (25)
_Daphnia rosea_* (15)
_Daphnia longiremis_* (16)
Daphnia sp.* (10)
Diaphanosoma sp.* (17)
_Leptodora kindtii_* (9)
_Sida crystallina_* (8)
_Ceriodaphnia reticulata_* (3)
Daphnia middendorffiana (< 3)
Daphnia retrocurva (< 3)
Daphnia catawba (< 3)
Daphnia (juvenile) (< 3)
Polyphemus pediculus (< 3)
Latona parviremis (< 3)

Copepoda Calanoida
_Leptodiaptomus minutus_* (36)
_Leptodiaptomus sicilis_* (8)
_Leptodiaptomus ashlandi_* (3)
_Skistodiaptomus oregonensis_* (5)
_Epischura lacustris_* (21)
Copepodid calenoïds* (53)
Limnocalanus macrurus (< 3)
Leptodiaptomus siciloides (< 3)

Copepoda Cyclopoida
_Diaptomus bicuspidatus thomasi_* (19)
_Mesocyclops edax_* (21)
_Tropocyclops prasinus mexicanus_* (4)
_Cyclops scutifer_* (21)
_Cyclopoid copepodids_* (45)
Eucyclops serrulatus (< 3)

Copepoda Naupii* (54)

Phytoplankton (No)

Microflagellates
Chlorophytes
_Selenastrum minutum_* (40)
_Ankistrodesmus falcatus_* (23)
Oocystis sp.* (37)
_Oocystis pulsilla_* (6)
_Dictyosphaerium ehrenbergianum_* (19)
Gloeocystis sp.* (24)
_Crucigenia tetrapedia_* (16)
_Tetraedron minimum_* (23)
Mougeotia sp.* (6)
Crucigenia sp.* (7)
_Pediastrum tetras_* (6)
_Arthrodesmus incus_* (23)
Scenedesmus sp.* (9)
_Elakatothrix gelatinosa_* (17)
_Closteriopsis longissima_* (6)
Cosmarium sp.* (18)
Quadrigula sp.* (25)
_Botryococcus sudeticus_* (7)
_Botryococcus braunii_* (7)
_Oocystis crussa_* (39)
Scenedesmus denticulatus (4)
Micrasterias sp. (3)
Oocystis parva (3)
Stauratrum sp. (4)
Staurastrum pentacerum (3)
Euastrum sp. (4)

Pyrrophytes
Peridinium sp.* (20)
_Peridinium inconspicum_* (11)
Ceratium hirundinella (4)
Gymnodinium sp. (3)

Chrysophytes
Kephyrion sp.* (7)
Mallomonas sp.* (37)
Desmarella sp.* (8)
_Bitrichia chodati_* (41)
_Dinobryon crenulatum_* (8)
_Dinobryon bavaricum_* (41)
_Dinobryon sertularia_* (17)
Dinobryon sp.* (20)
_Chrysosphaerella longispin_a* (7)
_Rhizosolenia eriensis_* (22)
_Asterionella formosa_* (36)
_Tabellaria floculosa_* (18)
_Tabellaria fenestrata_* (35)
_Synedra nana_* (16)
_Synedra ulna_* (7)
_Eunotia sp._* (7)
_Navicula sp._* (18)
_Stephanodiscus sp._* (8)
_Nitzschia sp._* (13)
_Melosira italica_* (14)
_Cyclotella sp._* (20)
_Hyalobryon musuola_* (6)
Mallomonas akrokonos (4)
Melosira distans (4)
Melosira sp. (4)
Chrysolykos skujae (5)
Synedra sp. (5)

Phytoplankton (No) (cont'd)

Synedra acus (5)
Bicoeca sp. (3)
Diatoma elongatum (3)
Epiphyxis sp. (4)
Surirella sp. (3)

Cyanophytes
_Anabaena flos-aquae_* (9)
_Oscillatoria limnetica_* (11)
_Aphanocapsa delicatissima_* (25)
_Anabaena sp._* (9)
_Coelosphaerium sp._* (9)
_Aphanothece clathrata_* (10)
_Merismopedia tenuissima_* (29)
_Chroococcus limneticus_* (17)
_Chroococcus dispersus_* (36)
_Dactylococcopsis smithii_* (6)
_Aphanocapsa elachista_* (26)
_Aphanothece nidulans_* (50)
_Microcystis sp._* (10)
_Chroococcus sp._* (10)
_Aphanocapsa sp._* (11)
_Merismopedia minima_* (29)
_Dactylococcopsis acicularis_* (36)
Cylindrospermum sp. (3)
Merismopedia glauca (3)
Rhabdoderma lineare (3)
Microcystis incerta (4)
Lyngbia limnetica (5)
Mycrocystis aeruginosa (3)
Holopedium irregulare (3)
Gomphosphaeria sp. (5)

Fish (No)

Catostomids
_Catostomus commersoni_* (24)
_Catostomus catostomus_* (14)
Catostomus sp. (2)

Salmonids
_Salvelinus fontinalis_* (22)
_Salvelinus namaycush_* (4)
Salvelinus alpinus (1)
_Coregonus clupeaformis_* (13)
Coregonus artedii (1)

Percids
_Perca flavescens_* (8)
_Stizostedion vitreum_* (13)

Esocid
_Esox lucius_* (21)

Others
Osmerus mordax (1)
Micropterus dolomieui (2)
Lotta lotta (1)
Semotilus corporalis (6)
Couesius plumbeus (1)
Anguilla rostrata (1)
Cyprinidae (6)