Dietary Variation in a Freshwater Fish Species: Relative Contributions of Biotic Interactions, Abiotic Factors, and Spatial Structure[1]

Pierre Magnan and Marco A. Rodríguez[2]

Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada

Pierre Legendre

Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, QC H3C 3J7, Canada

and Sylvain Lacasse

Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada

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We used multivariate analyses to examine which variables among the environmental and spatial components can best account for dietary variation in a freshwater fish, brook trout, *Salvelinus fontinalis*. The diet composition of brook trout was quantified in 37 lakes of the Laurentian Shield, Québec, Canada. Among the 25 measured environmental variables, fish species composition, sampling date, macrophyte abundance, and trout body length were the best predictors of diet composition. The total variation in diet composition was partitioned into four components: pure environmental 21.6%, pure spatial 23.2%, shared 19.9%, and unexplained 35.3%. A significant spatial trend in diet composition existed even after accounting for the main effects measured by the environmental variables. The two sets of spatial variables, when combined with the environmental descriptors, extracted different components of the dietary variation. The study allowed us to (1) highlight the role of spatial structure in diet variation of brook trout, (2) determine the relative contribution of both environmental and spatial components, and (3) generate testable hypotheses concerning mechanisms underlying the observed structure. Dependent variables other than diet composition, such as the density of different species at different sampling sites, can be used within the same statistical framework in studies of community ecology.

Nous avons utilisé des analyses multivariées pour déterminer quelles variables, parmi les composantes spatiale et environnementale, peuvent le mieux rendre compte de la variation dans l'alimentation d'une espèce de poissons d'eau douce, l'omble de fontaine, *Salvelinus fontinalis*. L'alimentation de l'omble de fontaine a été quantifiée dans 37 lacs du bouclier laurentien, Québec, Canada. Parmi les 25 variables environnementales mesurées, la composition en espèces de poissons, la date d'échantillonnage, l'abondance des macrophytes et la longueur des ombles ont été les meilleurs prédicteurs de l'alimentation. La variation totale de l'alimentation se distribuait à l'intérieur de quatre composantes : environnementale pure 21,6 %, spatiale pure 23.2 %, partagée 19,9 % et inexpliquée 35,3 %. Une tendance spatiale significative dans l'alimentation était toujours présente même après avoir tenu compte des effets principaux mesurés par les variables environnementales. Les deux ensembles de variables spatiales, lorsque combinés avec les descripteurs environnementaux, extrayaient différentes composantes de la variation de l'alimentation. Cette étude nous a permis de 1) mettre en lumière le rôle de la structure spatiale dans la variation de l'alimentation de l'omble de fontaine, 2) déterminer la contribution relative des composantes spatiale et environnementale et 3) générer des hypothèses testables concernant les mécanismes qui sous-tendent les structures observées. La composition de l'alimentation d'une espèce de poissons, l'omble de fontaine, a été utilisée comme variable dépendante dans nos analyses. Cependant, d'autres variables dépendantes, comme la densité de différentes espèces à différents sites d'échantillonnage, peuvent être utilisées à l'aide du même cadre statistique dans l'étude de l'écologie des communautés.

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Ecology is concerned not only with describing the patterns of distribution and abundance of species within communities, but also with determining the factors which are responsible for these patterns. It is now well recognized that biotic and abiotic factors may act jointly in structuring populations and communities (Schoener 1982; Danielson

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[1] Contribution of the Groupe de recherche interuniversitaire en limnologie (GRIL).

[2] Present address: Département de biologie et des sciences de la santé, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

1991; Dunson and Travis 1991; Norton 1991; Hart 1992). Although this pluralistic view is now well accepted, populations and communities are still often studied in a single-factor perspective, assuming that only one kind of factor (biotic or abiotic) plays a major role in structuring communities; these studies often focus on the effect of only one type of process (e.g., competition), presuming all other biotic and abiotic processes to have a neutral effect (Dunson and Travis 1991). Such an approach is not only biased, it also yields no information on the relative contributions of the biotic and abiotic factors or their interactions. When such interactions are not considered, one may overemphasize or misinterpret the effects of one or more factors, especially when these factors are intercorrelated (collinearity). Beyond the recognition that biotic and abiotic factors are jointly important in structuring communities, we need to evaluate which ones, among the biotic and abiotic variables, can best account for a given ecological structure such as the species abundances, or the pattern of resource use by species within communities. This is crucial not only to assess what are the most important variables, but also to determine which ones must be emphasized to better understand mechanisms underlying community organization (Schoener 1986; Persson and Diehl 1990).

It is also recognized that ecological patterns vary spatially. Regardless of habitat, components of population and community structure often exhibit consistent trends over environmental gradients (Menge and Olson 1990). Considering that biotic and abiotic factors vary spatially, another important issue in ecology is to determine the role of the spatial components in structuring populations and communities. Although ecologists have recently called for the inclusion of spatial structures in population and community investigations (see Ricklefs 1987; Legendre and Troussellier 1988; Bennett 1990; Menge and Olson 1990; Borcard et al. 1992; Levin 1992; Legendre 1993; Borcard and Legendre 1994), very few concrete approaches have been proposed. Furthermore, there is very little published work suggesting quantitative procedures for analyzing simultaneously the environmental (biotic and abiotic) and spatial components and determining their relative contributions in structuring a given ecological attribute such as the abundance or resource use of a species (e.g., Legendre and Troussellier 1988; Borcard et al. 1992).

The main objectives of this study are to determine (1) which variables, among the environmental and spatial components, can best account for diet variations in a freshwater fish species, the brook trout, *Salvelinus fontinalis*, and (2) what is the relative contribution (and statistical significance) of each of these components to the explained variance. A secondary objective is to suggest a statistical procedure, based on a combination of existing methods, which may be used to analyze the environmental and spatial components in population and community ecology. This procedure will also allow for the inclusion of a temporal component, which may be as important as the environmental and spatial components to explain variations in seasonally fluctuating environments (e.g., Bennett 1990).

Biological Background

The brook trout is found in sympatry with the northern redbelly dace, *Phoxinus eos*, the creek chub, *Semotilus atromaculatus*, and the white sucker, *Catostomus commersoni*, in many oligotrophic lakes of southern Québec, Canada. Cyprinids and catostomids were introduced in these lakes by bait fishermen 30–70 yr ago, or colonized these habitats after natural barriers disappeared following the use of splash dams for log transport, a practice commonly used at the beginning of the century (Bilby and Ward 1991; Lacasse and Magnan 1994). Brook trout colonized the area following the last glaciation (Lacasse and Magnan 1994). A survey done by the Québec Government in the 1970's revealed that among the 329 lakes found in our study area (Mastigouche and Saint-Maurice reserves; 45°73′N, 73°17′W), 41% contained allopatric brook trout populations (i.e., with no other fish species present), 33% contained trout and northern redbelly dace, 26% contained trout and creek chub, 20% contained trout and white sucker, and 20% contained more than two introduced species with brook trout (note that percentages do not add to 100 because there is overlap in category membership). These are typical small oligotrophic lakes with respect to surface area, mean depth, conductivity, Secchi disk transparency, thermal stratification, and oxygen concentration (Magnan 1988, 1989). All lakes in the present study are located within a 3000-km^2 area.

The impact of introduced species on brook trout populations has been investigated since 1978 in this study area, mainly by comparing allopatric brook trout with populations living sympatrically with introduced species. There is no lake in the area containing only dace, chub, or sucker. In this kind of study, comparisons are often done based on only one unit of each type of community. A major criticism of this approach is that comparisons that use single sampling units (here, lakes) may not always be valid because observed differences may be due to factors other than the presence or absence of a given species (Sale 1979; Diamond 1986). In order to minimize this potential source of error, some authors have made comparisons on replicates of allopatric and sympatric brook trout populations (Magnan and FitzGerald 1982; Magnan 1988; Lachance and Magnan 1990a, 1990b; East and Magnan 1991; Magnan and Stevens 1993; Rodríguez and Magnan 1993). Another approach has been to study different kinds of dependent variables (e.g., components of brook trout diet, density, biomass, and mean length of planktonic prey in the resource) using multiple linear regression models (Lacasse and Magnan 1992; Rodríguez et al. 1993). More detailed studies investigating spatial distributions of the fish, as well as their feeding habits in terms of prey type, prey size, and seasonal variation, have been done on subsets of the lakes (Magnan and FitzGerald 1982, 1984a; Naud and Magnan 1988; Tremblay and Magnan 1991). Finally, studies investigating foraging and aggressive behavior of the fish have been conducted in the laboratory, in order to explain specific results obtained in the field (Magnan and FitzGerald 1984b; East and Magnan 1991).

The presence of creek chub and white sucker significantly reduces the sportfishing yield (kilograms per hectare per year) of brook trout (Magnan 1988). Gillnet fishing and field experiments have revealed that the relative abundance of brook trout, in terms of catch per unit of effort, is significantly lower in lakes containing white sucker in which most of the mortality occurs in the period between hatching (in April) and the beginning of June (Lachance and Magnan 1990a; Venne and Magnan 1995). One of the most striking effects of competing species involves the feeding habits of brook trout (Magnan and FitzGerald 1982; Magnan 1988; Lachance and Magnan 1990b; East and Magnan 1991; Tremblay and Magnan 1991; Lacasse and Magnan 1992). In allopatry, brook trout feed mostly on benthic invertebrates of the littoral zone, e.g., Diptera, Trichoptera, Megaloptera (Sialidae), Ephemeroptera, and Odonata. In contrast, trout living in sympatry with creek chub and white sucker shift their food habits to prey found in the pelagic zone (open water) such as zooplankton (mostly *Daphnia* and *Holopedium*), swimming and emerging aquatic insects, dipteran pupae, terrestrial insects, and, to some extent, prey fish (almost exclusively northern redbelly dace). This diet shift of sympatric brook trout is correlated with a shift in their spatial distribution within lakes (Magnan and FitzGerald 1982; Tremblay and Magnan 1991), with significant changes in gill rakers and pyloric caecal morphology (Magnan 1988; Magnan and Stevens 1993), and with significant changes in the structure of the zooplankton community (Magnan 1988; Rodríguez et al. 1993). Creek chub and white sucker, which feed mostly on benthic invertebrates, appear to be better adapted (morphologically and behaviorally) than brook trout to feeding on bottom prey (Magnan and FitzGerald 1984b; Magnan 1988; Tremblay and Magnan 1991).

Between May and July, the benthic resources tend to decrease in abundance (Magnan and FitzGerald 1982; Tremblay and Magnan 1991; Rodríguez and Magnan 1993). Competition between brook trout and introduced species for benthic resources is stronger when food is scarce; therefore, as summer advances, trout feed more intensively on the open-water prey and less on benthos. Another factor that should contribute to this seasonal shift of trout to the pelagic zone is the increase of water temperature in the littoral zone during the summer (Tremblay and Magnan 1991). This may have more of an influence on trout than on sucker because of their different thermal preferendum (16.1°C for brook trout versus 21.0°C for white sucker; Wismer and Christie 1987).

For all the response variables for which we have compared the effects of creek chub and white sucker (yield, feeding habits, length of the gill rakers of brook trout, zooplankton community structure), the impact of sucker tends to be stronger than that of chub. This could be explained by the fact that white sucker may use significant amounts of zooplankton, which is the main competitive "refuge" along the food axis for trout in these lakes. Small white sucker (1.3–2.3 cm) are planktivorous (Carlander 1969; Scott and Crossman 1973), and larger ones may feed heavily on cladocerans, especially late in the summer (Tremblay and Magnan 1991).

Multiple linear regression analyses have indicated that the presence of introduced species is not the only determinant of the diet of brook trout; for example, the independent variables, presence of chub and sucker, zooplankton community structure, sampling date, morphoedaphic index, and importance of rock outcrops, accounted for 88% of the variation in mass of zoobenthos eaten by trout, which was the preferred prey in allopatry (Lacasse and Magnan 1992). In another model, 30% of the variation in mass of zooplankton eaten by trout was explained by the importance of macrophytes and refuges for fish (trout or their prey). Models for the abundance of amphipods, dipteran pupae, swimming insects, terrestrial insects, and prey-fish in the diet explained between 36 and 63% of the variation; the presence of white sucker or an index of their impact (mean length or density of Cladocera) and at least two habitat characteristics (e.g., pH, transparency, slope, morphoedaphic index, rocks and rock outcrops, emergent vegetation, macrophyte importance, and refuge for fish) appeared in each of these models (Lacasse and Magnan 1992).

The Approach

Community data typically involve numerous sites and species, which naturally lead one to rely on multivariate analyses to summarize the data while minimizing distortion of the spatial arrangement of sites or species (Gauch 1982; Legendre and Legendre 1983; Pielou 1984; Jackson et al. 1992). Conventional clustering and ordination methods are powerful tools for pattern detection and for synthesizing multivariate ecological data, but these methods are limited in their ability to detect relationships between community attributes and predictor variables and to assess the statistical significance of putative relationships. This can lead to overinterpretation of patterns that are not biologically or statistically significant (Jackson et al. 1992).

In the following section, a flexible and general statistical framework is presented that can be used to estimate the effects of independent environmental and spatial variables on multivariate community attributes and to assess the statistical significance of these relationships. In the first step of our analysis, the trout diet composition, which we have quantified in different lakes, was related to three sets of predictor variables separately: environmental (biotic and abiotic), geographic coordinates, and drainage pattern; these last two sets represent different ways of looking at the spatial organization of our fish populations. Each set of variables (diet, environmental, and spatial) was represented as a "variable by lake" matrix. Then in a second step, to determine whether the interpretation of trout diets on the basis of environmental variables could be enhanced by inclusion of the spatial structure (geographic location or drainage pattern), the total variation in trout diet composition was partitioned into independent components representing the relative contributions of the different sets of predictor variables. Used in combination with permutation tests, this procedure allowed us to evaluate the magnitude and statistical significance of effects associated with each component.

Materials and Methods

We used the same environmental and diet data as Lacasse and Magnan (1992), while spatial variables were quantified specifically for this study. Detailed information on the study area, field methods, and laboratory procedures can be found in Lacasse and Magnan (1992). Therefore, only a brief summary is presented here.

Study Lakes

Data on trout diet were collected in 42 lakes in the Mastigouche Reserve, Québec (46°40′N, 73°20′W). Analyses relating diet composition to environmental variables were performed only on the 37 lakes for which complete sets of environmental data were available. The study lakes were assigned to three major types according to fish species composition (Magnan 1988; Lacasse and Magnan 1992). Among the

37 lakes, 12 contain brook trout ("trout" lakes), 12 contain brook trout and creek chub ("chub" lakes), and 13 contain brook trout and white sucker ("sucker" lakes). Creek chub and pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*) are also present in some of the sucker or chub lakes, but their relative biomass is less than 1% in these lakes (Magnan 1988). Northern redbelly dace is found in most of the lakes but does not affect the mean yield of brook trout in the study area (Magnan 1988).

Trout Diet Composition

Stomachs (a mean of 20 per lake) were sampled from brook trout captured during daytime by anglers between 1 and 30 June 1989. The mean percent wet mass (Hyslop 1980) of each of nine functional prey categories, reflecting differences in microhabitat utilization, was recorded in the laboratory: zoobenthos (mostly Diptera, Ephemeroptera, Odonata, and Trichoptera larvae), amphipods (mostly Gammaridae), zooplankton (mostly Cladocera and Chaoboridae), dipteran pupae, aquatic insects (Hemiptera and Coleoptera), terrestrial insects, prey-fish (mainly northern redbelly dace), leeches, and "other" prey items.

Environmental Variables

Lake maximum depth, surface area, volume, and perimeter were obtained from 1:20 000 bathymetric maps. Epilimnetic temperature at 0.5 m, conductivity, pH, and Secchi disk transparency were measured in the field, as were the percentages of the shoreline containing submerged wood, herbs, shrubs, beach, mudflats, rocks, and rock outcrops. Macrophyte abundance was coded as an ordinal index from 0 to 5. Temperature profiles and bathymetric maps were used to estimate the area contained within the thermal optimum zone (13–17°C) for brook trout (Lacasse and Magnan 1992). A binary variable was used to code whether the littoral zone overlapped the thermal optimum. The numerical density, biomass, and mean length of cladocerans were estimated from triplicate samples collected in midlake. Mean fork length was used as a measure of brook trout size. Sampling date, within the month of June 1989, was included as an environmental covariable to account for seasonal trends over the sampling period. Fish species composition was coded using three binary dummy variables, TROUT, CHUB, and SUCKER, to label the three lake types "trout", "chub", and "sucker" as follows:

	Dummy variable		
Lake type	TROUT	CHUB	SUCKER
Trout	1	0	0
Chub	0	1	0
Sucker	0	0	1

Although in general, only two categorical variables are required to distinguish among three categories (Montgomery and Peck 1982), this particular coding is used by program CANOCO (ter Braak 1990a). This is more appropriate than coding trout = 1, chub = 2, and sucker = 3 because the latter coding arbitrarily imposes a potentially misleading ordering of treatment effects (Montgomery and Peck 1982).

Spatial Variables

The geographic coordinates for the lake, as well as the pattern of interconnections among lakes, were obtained from 1:50 000 and 1:250 000 government maps. The matrix of two-dimensional geographic coordinates was completed, following Legendre (1990), by including all terms for a cubic trend surface polynomial; this procedure allows one to estimate the parameters of a trend surface regression equation of the form

$$Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$$

where X is longitude and Y is latitude in Cartesian coordinates. This equation represents a geographic surface that can be used to describe how a summary measure of the trout diet (the Z variable, which in this study takes the form of ordination axis scores) varies over the matrix of X–Y coordinates. Inclusion of quadratic, cubic, and interaction terms in the equation allows us to model not only simple linear gradient patterns but also more complex features such as patches or gaps (Borcard et al. 1992). Geographic coordinates were centered to zero mean before computing the higher terms of the polynomial to reduce nonessential collinearity when fitting the polynomial (Montgomery and Peck 1982).

The pattern of lake interconnections was quantified following the method proposed by Kluge and Farris (1969) for coding a character transformation series in phylogenetic analysis. The procedure can be briefly summarized as follows. A hydrographic "tree" is built that maps the connections among lakes (Fig. 1). A node number is then assigned to each of the bifurcations or branching points in the tree. Each lake is characterized by the sequence of nodes along the direct path connecting the lake to the "root" or base of the tree. A lakes-by-nodes matrix is constructed by assigning, for each lake, a value of 1 to all nodes connecting it to the root and 0 to all other nodes. Two special cases deserve special attention. First, lakes forming a node (i.e., the lake receives inflows from more than one subbasin: nodes 5, 6, 17, and 26 in Fig. 1) were coded 0 for that node because it is not located downstream from that lake. Second, lakes positioned on branches between two bifurcations (e.g., the three lakes along the minor branch created by node 10 in Fig. 1, or the lakes between nodes 16 and 17) were not given special node numbers and were assigned the same node values because all these lakes belong to the same subbasin. The matrix resulting from this procedure contains a complete numerical coding of the drainage basin pattern depicted by the hydrographic tree.

Statistical Framework

Trout diet composition was related to the three sets of predictor variables separately (environmental, geographic coordinates, and drainage pattern) by canonical correspondence analysis (ter Braak 1986), an eigenvalue ordination technique especially designed for direct analysis of the relationships between multivariate ecological data tables. Ordination scores were used to create a scattergram that simultaneously represents the dietary items, the environmental variables (biotic and abiotic), and the study lakes. For each set of independent variables, the best predictors were selected using a forward selection procedure available in version 3.1 of program CANOCO (ter Braak 1988b; program available from C.J.F. ter Braak, Agricultural Mathematics Group, TNO Institute for Applied Computer Science, Box 100, NL-6700 AC Wageningen, The Netherlands), with a cutoff point of $p = 0.10$.

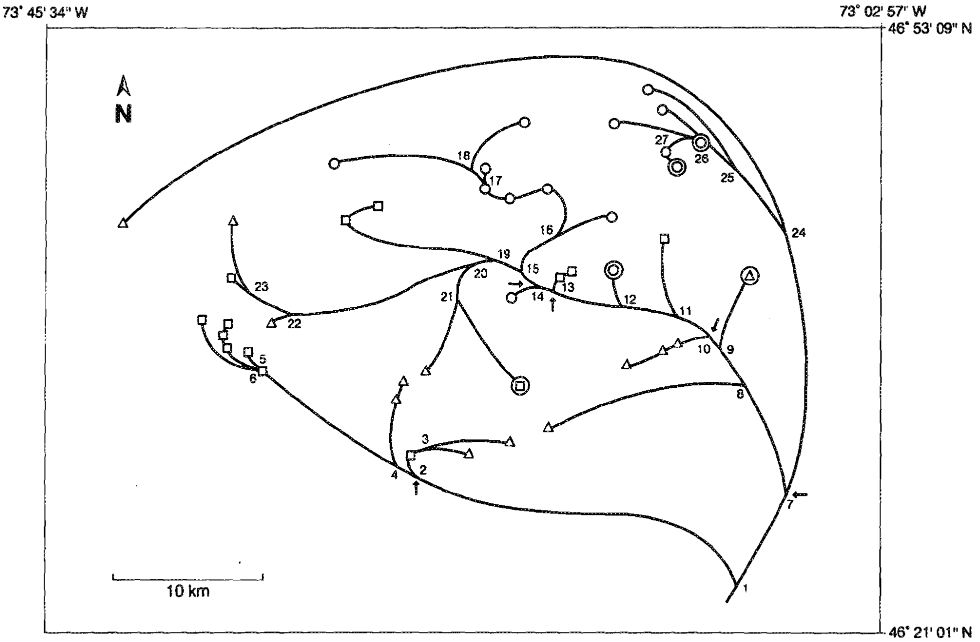

FIG. 1. Schematic representation of geographic locations and interconnections among the study lakes. Lakes enclosed by a circle were not included in canonical correspondence analyses (see Materials and Methods). Circles, trout lakes; triangles, chub lakes; squares, sucker lakes. Numbers (1–27) represent nodes of the hydrographic network (see Materials and Methods: Spatial Variables).

Multivariate tests for overall differences in diet composition among lake types were made with canonical correspondence analysis, using only as predictor variables the dummy variable coding for fish species composition, as described by ter Braak (1987).

Following the study of trout diet composition as a function of the three sets of predictor variables separately, trout diet variation was analyzed against the environmental and spatial variables together, using the method of variation partitioning proposed by Borcard et al. (1992) and Borcard and Legendre (1994). The purpose now is to determine whether interpretation of trout diets on the basis of environmental variables could be enhanced by inclusion of the spatial structure (geographic location or drainage pattern); following this analysis, the total variation in trout diet composition was partitioned into four independent components ("pure" environmental, "pure" spatial, spatial component of environmental variation, and unexplained) by canonical and partial canonical correspondence analysis (ter Braak 1986, 1988a). This procedure involves the following steps: (1) compute the variation accounted for by the environmental variables; (2) compute the variation accounted for by the spatial variables; (3) compute the variation explained by the environmental variables after removing by partial canonical correspondence analysis the effect of the spatial variables; (4) compute the variation explained by the spatial variables after removing the effect of the environmental variables by partial canonical correspondence analysis. The total explained variation (r^2) is the sum of the explained variations in (1) and (4) or in (2) and (3). The nonspatial ("pure") environmental variation is given by step (3), and the ("pure") spatial variation that is not related to the environmental variables is given by step (4). The spatially structured environmental variation, or variation "shared" by the spatial and environmental variables, is obtained by subtracting (3) from (1) or (2) from (4). The unexplained portion of variation is obtained by subtracting the "pure" environmental variation, the "pure" spatial variation, and the "shared" variation from the total variation. Variation partitioning was performed in two parallel sets of analyses, one including environmental variables and geographic coordinates and another including environmental variables and drainage pattern. Then, to determine whether the two sets of spatial variables extracted different (nonoverlapping) components of the dietary variation, an extension of this method, incorporating simultaneously the three sets of explanatory variables, was used to partition the total variation. The statistical significance of the environmental and spatial components was evaluated by Monte Carlo permutation tests of the sum of all eigenvalues, as implemented in CANOCO.

Results

Overall, the dietary items were found in the following relative abundances: zoobenthos (43.8%), zooplankton (23.6%), aquatic insects (7.2%), dipteran pupae (6.9%), terrestrial insects (6.2%), prey-fish (5.2%), others (2.6%), amphipods (2.6%), and leeches (1.9%).

Environmental Variables

Among the 25 environmental variables initially considered for inclusion in the canonical correspondence analyses, only five were retained by the forward selection procedure: macrophyte abundance, the dummy variable trout (which separated trout lakes from chub lakes and sucker lakes), sampling date (within the same month), pH, and mean fish length. None of the pairwise correlations among these five environmental variables exceeded 0.19. Combined, these five variables account for 41.6% of the total variation in trout diet composition. The first ordination axis extracted by canonical correspondence analysis accounts for 16.3% of the variation; it

TABLE 1. Summary statistics for canonical correspondence analysis of brook trout diet and environmental variables. Eigenvalues were 0.165 for axis 1 and 0.115 for axis 2. $*p < 0.05$.

	Canonical coefficients		Correlations with canonical axes	
	Axis 1	Axis 2	Axis 1	Axis 2
Date	0.26*	−0.03	0.48*	−0.16
Macrophytes	0.07	−0.29*	0.19	−0.62*
pH	0.04	−0.12	−0.04	−0.31
Fish length	−0.15*	−0.09	−0.31	−0.20
Trout lake	−0.26*	−0.08	−0.52*	−0.25

TABLE 2. Canonical coefficients for individual predictor terms in analyses with spatial variables as predictors. In the geographic coordinate analysis, eigenvalues were 0.111 for axis 1 and 0.066 for axis 2; in the drainage pattern analysis, eigenvalues were 0.210 for axis 1 and 0.110 for axis 2. $*p < 0.05$.

Geographic coordinates			Drainage pattern		
Predictor	Axis 1	Axis 2	Predictor	Axis 1	Axis 2
X	0.34*	0.17	Node 2	0.13	0.29*
Y	−0.30*	0.09	Node 10	0.67*	−0.01
X^2	0.22	−0.23	Node 13	−0.28	0.48*
Y^2	−0.17*	0.01	Node 14	−0.37*	−0.34*
X^3	0.03	−0.47*			

primarily reflects differences due to fish species composition, seasonal change, and fish length (Table 1). The second axis accounts for an additional 12.7% of the variation and reflects a gradient in pH and macrophyte abundance (Table 1). Diet composition and environmental variables are significantly related ($p = 0.001$), as shown by a Monte Carlo permutation test (1000 permutations) for the sum of all canonical eigenvalues (ter Braak 1990a).

Representation of lakes, dietary items, and environmental variables on an ordination diagram (Fig. 2) shows that 33 of the 37 lakes are grouped into an elongated cluster that runs from center-left to bottom-center of the graph, diagonal to axes 1 and 2. A cluster analysis (not presented here) performed on the coordinates for the first two ordination axes (UPGMA algorithm based on Euclidean distance, misleadingly called "average linkage" in the SYSTAT program; Wilkinson 1990) clearly separated the lakes in the elongated cluster from the four outlying lakes. These four lakes lie outside the cluster mainly because of the high percentage of prey-fish consumed by brook trout in these lakes, as indicated by the symbol for prey-fish in the ordination plot and by direct comparison with percent consumption (26–46%, in contrast with 0–12% for all other lakes). High consumption of prey-fish in these lakes is related to high macrophyte abundance and late collection of samples (Fig. 2). Approximate t-tests (ter Braak 1990b) yielded significant results ($p < 0.05$) for both relationships. None of the other environmental variables was related significantly to consumption of prey-fish. The graph also indicates that amphipods were consumed more often in lakes with high macrophyte abundance ($p < 0.05$).

The most salient contrast in diet composition among the 33 lakes in the elongated cluster (Fig. 2) is between lakes in which zoobenthos is the major diet item (upper left of cluster) and those in which zooplankton, overall the second most abundant diet item, is consumed together with alternative prey (lower right of cluster). This contrast is most strongly associated with the dummy variable trout lake, as indicated by the alignment of the main axis of the cluster and the arrow for trout and by the length of this arrow (Fig. 2). The presence of creek chub or white sucker seems to cause a marked shift from zoobenthos, the dominant food item in trout lakes, to alternative prey; also, this shift becomes more pronounced as summer progresses, from 1 to 30 June. This interpretation, based on the ordination plot, is confirmed by direct comparison of percent consumption: zoobenthos accounts for an average of 60.3% of stomach contents in trout lakes (>50% in 11 of 15 lakes) whereas zoobenthos content averages 34.6% in chub and sucker lakes combined (>50% in 7 of 27 lakes).

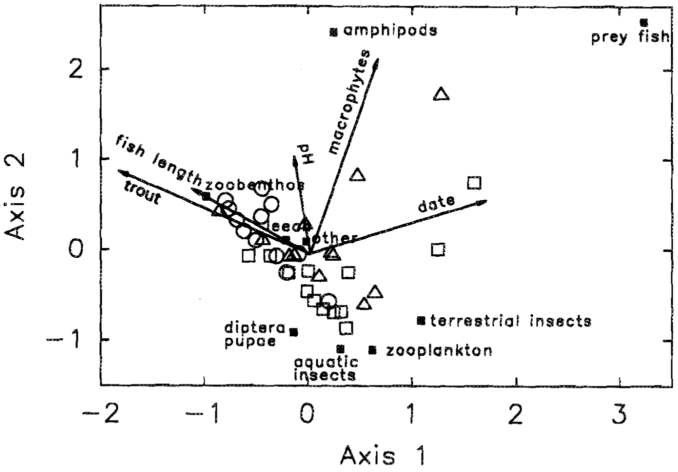

FIG. 2. Canonical correspondence ordination of lakes, diet items, and environmental variables. Open circles, trout lakes; open triangles, chub lakes; open squares, sucker lakes. Diet items are represented by solid squares. The environmental variable arrows are drawn from the centroid of the lake dispersion.

Spatial Variables

The best model relating diet composition to geographic coordinates accounts for 30.4% of the total variation and includes five terms after forward selection:

$$Z = b_1X + b_2Y + b_3X^2 + b_4Y^2 + b_5X^3.$$

Axis 1 accounts for 13.2% of the variation and axis 2 accounts for an additional 7.0% of the variation. The main dietary items providing contrast among lakes along axis 1 (determined mostly by terms X, Y, and Y^2; Table 2) are zoobenthos, which has the largest negative score, and prey-fish and terrestrial insects, which have large positive scores (Table 3). For axis 2 (determined mostly by term X^3; Table 2), the strongest contrast is provided by zooplankton versus prey-fish (Table 3).

The best model relating diet composition to the drainage pattern accounts for 29.5% of the total variation and includes nodes 2, 10, 13, and 14 (Fig. 1) as predictor terms, after forward selection; node 2, which is redundant with node 7 because all lakes included in node 2 are excluded from

TABLE 3. Ordination scores for dietary items in canonical correspondence analyses with spatial variables as predictors.

	Geographic coordinates		Drainage pattern	
	Axis 1	Axis 2	Axis 1	Axis 2
Zoobenthos	−0.78	−0.71	−0.66	−0.64
Amphipods	0.12	0.83	0.62	−3.34
Zooplankton	0.21	1.53	−0.15	0.80
Dipteran pupae	−0.41	0.50	−0.09	1.65
Aquatic insects	0.48	0.60	0.32	1.20
Terrestrial insects	1.15	−0.16	1.34	0.54
Prey-fish	3.26	−1.66	3.42	−0.88
Leeches	−0.16	−0.98	−0.30	−1.53
Other	0.32	0.13	0.04	−0.16

node 7 and vice versa, was eliminated by the forward selection procedure. Axis 1 accounts for 17.7% of the variation and axis 2 accounts for an additional 8.0% of the variation. The main dietary items providing contrast among lakes along axis 1 are zoobenthos and leeches versus prey-fish and terrestrial insects (Table 3). For axis 2, the strongest contrast is provided by amphipods and leeches versus dipteran pupae and aquatic insects (Table 3).

Components of Variation

Partitioning of the variation (Fig. 3) indicates that the environmental and the spatial variables together account for 56.8% of the total variation when the geographic coordinates are used and for 50.7% of the variation when the drainage pattern is used. The "pure" spatial component contributes substantially to the total variation (15.3% for geographic coordinates, permutational probability for the sum of all eigenvalues $p = 0.011$ after 1000 permutations; 9.2% for drainage pattern, permutational $p = 0.001$ after 1000 permutations), but still a relatively large portion of the total variation (43–49%) is left unexplained. The component of variation shared by the environmental and spatial variables is higher for the drainage pattern (20.2%) than for the geographic coordinates (15.1%).

The "pure" spatial component (15.3%; $p = 0.011$) associated with the geographic coordinates can be visualized by drawing on a map a series of isopleths that connect points with the same value for axis 1 (Fig. 4), as recommended by Borcard and Legendre (1994). The picture clearly illustrates the significant spatial trend (decrease in axis 1 scores along a west–northeast gradient) that remains in the diet data even after accounting for the main effects measured by our environmental variables. When these environmental effects are held constant by partial canonical analysis (see Materials and Methods), inspection of axis 1 scores for dietary items (given in parentheses) reveals that there was a tendency for relative abundance of amphipods (2.6) and of zooplankton (1.3) in the diet to be largest in lakes with high axis 1 values (west on the map) whereas prey-fish (−1.4), terrestrial insects (−1.6), dipteran pupae (−1.3), and leeches (−2.0) tended to be most abundant in diets of trout from lakes with low axis 1 values (northeast). Zoobenthos (−0.17), aquatic insects (0.18), and others (0.41) have intermediate values for axis 1.

In a partial canonical correspondence analysis controlling for the effect of both the environmental and drainage pattern variables, the geographic coordinates still explained a significant part (28.4%; permutational probability for the sum of all eigenvalues $p = 0.013$ after 1000 permutations) of the remaining variation in diet composition; this part is equal to 14.0% of the total variation. This demonstrates that the two sets of spatial variables, when combined with the environmental descriptors, extract different, largely nonoverlapping components of the dietary variation. A partition of the total variation using the three sets of explanatory variables (Fig. 5) revealed that the environmental variables combined with both sets of spatial variables account for 64.7% of the total variation. The portion of variation corresponding uniquely to the environmental variables (21.6%) is larger than the portions corresponding uniquely to either the geographic coordinates (14.0%) or the drainage pattern (7.9%). Most of the explained variation is accounted for by these three portions (43.5% of the total variation) plus the portion that is simultaneously shared by the three sets of explanatory variables (15.4% of the total variation) (Fig. 5). The negative value −0.3% in Fig. 5 results from calculation of variation components by difference, and should be interpreted as being approximately zero.

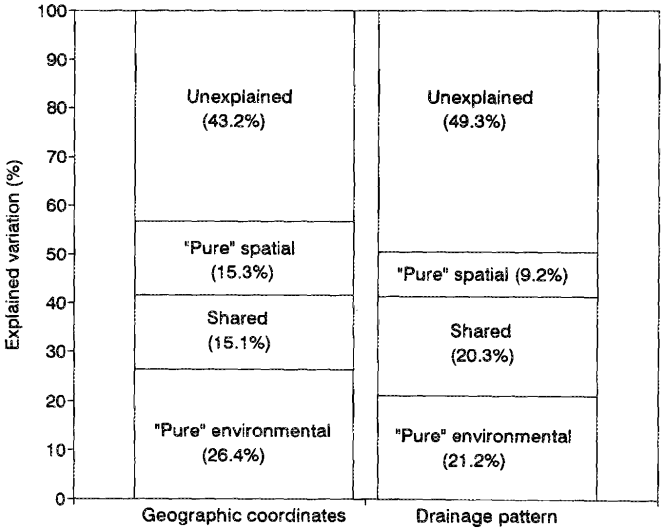

FIG. 3. Partition of the total variation in diet composition into four independent components: "pure" environmental, "pure" spatial, spatial component of environmental variation ("shared" variation), and unexplained. Left: Analysis with environmental variables and geographic coordinates as predictors. Right: Analysis with environmental variables and drainage pattern as predictors.

Discussion

The present study allowed us to highlight the role of the spatial structure in the dietary variation of brook trout and to determine the relative contributions of the environmental and spatial components to the observed structure. Outside of, and in addition to, the classical environmental control of species (according to Table 1, the most important environmental variables are fish species composition, date of sampling, macrophyte abundance, and trout body length), this study demonstrates that other geographically structured factors are at work. There may be, of course, spatially structured environmental variables that were not taken into account in our study, and these may be determinants of trout diet; or, this spatial structure may reflect trout genetic factors that happen

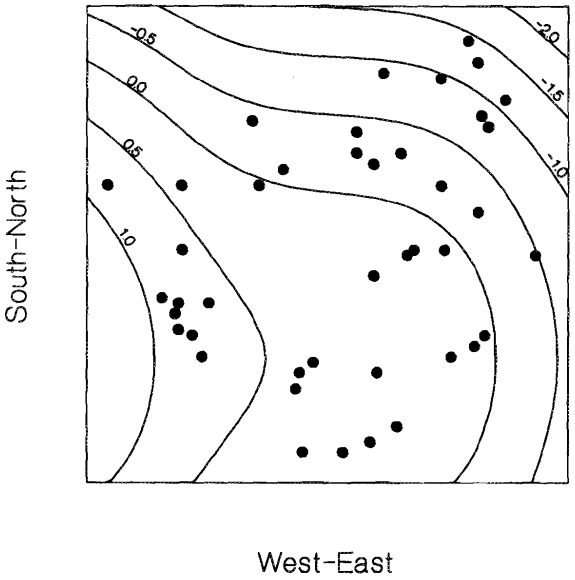

FIG. 4. Geographic map representing the "pure" spatial variation in diet composition (from the geographic coordinate analysis). Each point represents a lake. The curves are fitted isopleths for axis 1 values (see Results).

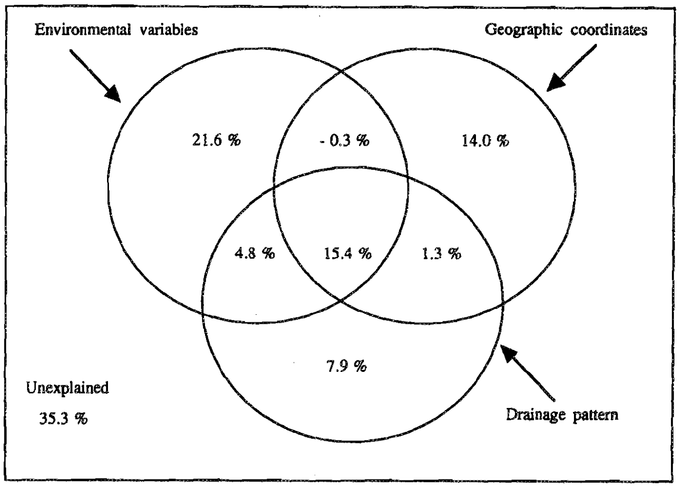

FIG. 5. Venn diagram showing the partition of the total variation in diet composition explained by the three sets of explanatory variables. The negative value −0.3% results from calculation of variation components by difference, and should be interpreted as being approximately zero.

to have a spatial structure because of historical events such as dispersal of species through the river drainage system or of introduction of bait species from roadways (details below). Before the present study, although the effect of the environmental component (biotic and abiotic factors) on brook trout diet had been documented in the system under study here, nothing was known concerning the spatial structure of this response variable or the interaction between the environmental and spatial components.

With regard to the role of the environmental variables, the results of the present analysis were consistent with studies previously undertaken in the same study system (see section describing the system). Moreover, because the present analysis simultaneously related all the components of fish diet with the environmental variables, which had not been done in these previous studies, it was possible to determine the relative contribution of the different independent biotic and abiotic variables (as indicated in the ordination analysis by the alignment of the main axis of the cluster and the arrows of the different variables, and by the length of these arrows). The presence of creek chub or white sucker caused a marked shift from zoobenthos, the dominant food item in allopatry, to zooplankton and other alternative prey; this shift became more pronounced as the summer progressed. Also, high consumption of prey-fish was related to high macrophyte abundance and late sampling date. Finally, the occurrence of amphipods in the diet was related to pH and to macrophyte abundance. Together, these environmental variables accounted for 41.6% of the total variation in trout diet composition.

In addition to determining the portion of variation explained by the environmental variables, it is important to interpret the role of these variables in structuring communities. Although the above results appear to have ecological significance (e.g., see East and Magnan 1991; Tremblay and Magnan 1991; Lacasse and Magnan 1992), one must be cautious in interpreting the causal relationships between dependent and independent variables retained in the analysis. The latter are selected by a forward selection procedure on the basis of proportion of variance explained and statistical significance (ter Braak 1990a). Therefore, such an analysis should be viewed as preliminary to a mechanistic approach, providing support and guidance for the investigation of more realistic variables in mechanistic studies. The mechanistic approach, through field or laboratory experiments, has been proposed as the most promising one for addressing functional proximal relationships and enabling ecologists to better understand community patterns (Schoener 1986; Dill 1987; Persson and Diehl 1990). The use of this approach, however, requires some previous understanding of the potential key factors structuring a given system.

Even though our sampling strategy was not specifically designed to investigate the temporal component, results show that a temporal effect can be identified from our analysis; the date of sample collection has a significant effect on the trout diet, suggesting an influence of seasonality in resource availability or physiological requirements of the fish (e.g., temperature). In a study extending over a longer period in the summer season (May–August), Tremblay and Magnan (1991) showed that the niche shift of brook trout from littoral zone zoobenthos to pelagic prey was related to a decrease of food supply and an increase of temperature in the littoral zone.

The geographical coordinates and drainage pattern analyses showed that variation of trout diet composition among the 37 study lakes is spatially structured, i.e., that spatial variables explained an independent part of the diet variation after removal of the effect of measured environmental variables. In fact, the "pure" spatial component presumably reflects the effects of environmental variables that are spatially structured. The model based on geographic coordinates accounted for 30.4% of the total diet variation whereas the model based on drainage pattern accounted for 29.5%. Such a spatial structure could reflect phenotypic or genotypic differences in brook trout populations. Variation in diet explained by the drainage pattern may be the result of dispersal of introduced species in the different drainage subbasins. Another nonexclusive hypothesis is that variation in diet explained by the drainage pattern may be the result of geographic isolation between brook trout in the different subbasins, which could have led to long-term genetic differentiation. In contrast, variation in diet explained by geographic coordinates could have been the result of the pattern of baitfish introductions by anglers in these lakes, although their further dispersal could have been affected by drainage pattern. Actually, chub and sucker introductions must have occurred in lakes that were accessible by roads; this, in turn, is more a function of geography than of drainage pattern. As it is known that phenotypic changes have occurred in brook trout morphology (gill rakers and pyloric caeca) following these introductions (Magnan 1988; Magnan and Stevens 1993), it is possible that spatial variation in trout diet is related to the pattern of fish introductions. Although it would have been possible to incorporate some measure of accessibility such as distance from the road in our statistical analyses, interpretation of results would have been complicated by the fact that the road network has changed a great deal during the last century, in response to forest exploitation. Thus, present accessibility does not necessarily reflect past accessibility.

It is also possible that for a given introduced species, the trout has been in contact with genetically different populations, leading to different phenotypic responses. If this is the case, trout response can be measurable today in terms of both the drainage and geographical coordinate variables. The two methods of quantifying spatial structure will not always be simultaneously useful, or applicable to a given system. However, the drainage pattern method should always be used in combination with geographic coordinates when there is a network of connections between the sampling sites because the two methods can be complementary; this is the case, for instance, for creeks and streams connecting the lakes in this study, for valley networks facilitating dispersal of insects (M. Dufrêne, personal communication), or for land bridges connecting islands to the mainland through geological history (MacArthur 1972; Magnuson 1976). In addition to giving the portion of total variation accounted for by the spatial structure and permitting tests of statistical significance, our method of analysis allows one to frame testable functional hypotheses about the ecological significance of the spatial component.

The analysis showed that one can partition the total variation of the dependent variables (here, trout diet composition) into four independent components, "pure" environmental, "pure" spatial, shared, and unexplained, by using the procedure of Borcard et al. (1992). An extension of this method also allowed us to partition the total dietary variation among three sets of explanatory variables (environmental, geographic coordinates, and drainage pattern). The two sets of spatial variables extracted different, largely nonoverlapping components of the dietary variation (Fig. 5). This part of the analysis is efficient because it allows for simultaneous consideration of sets of environmental (biotic and abiotic) and spatial variables to account for dependent variables such as species density or resource use at different sampling sites. For example, Lacasse and Magnan (1992) built seven multiple regression models to predict the mean percent weight of seven components of brook trout diet from different biotic and abiotic variables; these models accounted for between 25.9 and 88.0% of the variation of given food items in the fish diet, which represents for most food items an overestimation of the importance of the environmental variables in structuring trout diet, compared with the results presented here. This overestimation probably owes to the fact that they modelled each of the seven components of the diet as if they were independent when in fact they are correlated (ter Brack and Prentice 1988). Using the same diet data that had been analyzed by Lacasse and Magnan (1992), the present analysis shows that the addition of spatial variables and the consideration of all components of the diet simultaneously can yield a different picture. If individual dietary components do not respond to the same composite gradient of environmental variables, the use of several regression models instead of ordination may allow for more detailed descriptions of the response of each dietary component to environmental variation (ter Braak and Prentice 1988; Rodríguez et al. 1993). However, this increase in detail also implies that overall, more environmental variables have to be included in the analysis. The approach used by Lacasse and Magnan (1992) retained more than 15 different environmental variables as predictors in seven separate regression models; in contrast, only five environmental variables were retained by the selection procedure in the present study. Among the environmental variables, differences in fish species composition appeared to be the major determinant of trout diet in the two studies. Nevertheless, our results suggest that the approach used by Lacasse and Magnan (1992) may have overestimated the *overall* effect on the diet of certain littoral habitat characteristics (e.g., variables reflecting littoral occupation of rock outcrops or refuge quality), which appeared in five of their seven models, and underestimated that of pH and of trout length, which appeared in only one model each. The overlap between the environmental and spatial components (Fig. 5) also suggests that a substantial part of the environmental effects detected in Lacasse and Magnan's (1992) study may in fact be interpretable as historical effects related to fish introductions, or to neglected (unmeasured) environmental variables that covary in space with the measured environmental variables retained by the selection procedure. The inclusion of the spatial component in our study led to testable hypotheses concerning introductions and dispersal of fish species (see above); such hypotheses are unlikely to arise naturally from studies that consider only the effect of the environmental component.

Our analysis used diet composition of brook trout as the dependent variable. Other dependent variables, such as population density, resource use, morphometric characteristics, or genotypic frequencies of, e.g., birds species on islands and the mainland, or of fish species at different stations along a coral reef, could be used within the same statistical framework in community ecology studies.

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