Spatial and temporal variation in littoral-zone fish communities: a new statistical approach

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Abstract: Through the use of principal coordinates analysis, a technique is presented that allows the quantitative partitioning of the total variation within a data set into its spatial and temporal components. The graphical nature of this technique, in combination with the quantitative results, aids in the examination of specific hypotheses regarding the structure of the variation. These hypotheses are tested against null or model matrices of the structure of the variation with statistical significance assessed using Mantel's test. This approach is applied to a data set of species' abundances from the littoral-zone fish communities of three Ontario lakes sampled three separate times. The variation was partitioned and the influence of different similarity measures was explored. Among-lake (spatial) variation accounted for 67–81% of the total variation. The time of sampling represented 1–3% of the total. There was significant among-lake variation for all three sampling periods whereas only one lake showed a significant temporal component. Together, both lake and time of sampling accounted for 74–86% of the variation, the remainder being within-lake variation (i.e., among-site or site-by-time interactions). The structure of the variation was sensitive to the similarity measure used as a result of differing emphasis on particular attributes (e.g., relative versus absolute abundance).

Résumé : Nous présentons une technique, qui s'appuie sur l'application de l'analyse des coordonnées principales, permettant de répartir quantitativement la variation totale, dans un ensemble de données, entre ses composantes spatiales et temporelles. Le caractère graphique de cette technique, allié à la présentation des résultats quantitatifs, facilite l'examen d'hypothèses spécifiques ayant trait à la structure de la variation. Celles-ci sont testées en fonction de matrices nulles ou de matrices modèles de la structure de la variation, et leur signification statistique est évaluée au moyen du test de Mantel. Cette démarche est appliquée à un ensemble de données sur l'abondance d'espèces appartenant à des communautés de poissons vivant en zone côtière dans trois lacs de l'Ontario où ont été pratiqués trois échantillonnages à des moments distincts. La variation a été répartie et l'influence de différentes mesures de similitude a été explorée. La variation (spatiale) entre les lacs correspondait à 67–81% de la variation totale. La date de l'échantillonnage expliquait 1–3% du total. Il existait une importante variation entre les lacs pour ce qui est des trois périodes d'échantillonnage alors qu'un seul lac avait une composante temporelle significative. Considérés ensemble, l'identité du lac et la date d'échantillonnage permettaient d'expliquer 74–86% de la variation totale, le reste étant attribuable à des variations à l'intérieur de chaque lac (c.-à-d. entre les stations ou en fonction d'interactions station-date d'échantillonnage). La structure de la variation était sensible au choix de la mesure de similitude du fait que l'accent se trouve mis sur différents attributs particuliers (p. ex., abondance relative ou abondance absolue).

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Introduction

Community structure and organization has a long history in ecological research. Current topics take many forms and include extensive work regarding the stochastic versus deterministic basis for community structure and random versus nonrandom patterns in communities (Schoener 1987). The identification of pattern in community data is a common problem with which community ecologists and biogeographers struggle (Jackson et al. 1992), yet the identification of pattern is a principal step that must be taken when examining community structure and organization. A complicating factor in such

studies is that community patterns may differ among spatial and (or) temporal scales or be random in nature. In a review of 489 studies of aquatic insects, Resh and Rosenberg (1989) concluded that the lack of consideration of spatial and temporal variation often occurs because simple, observable patterns arise more readily from a "homogenization" of the data spatially or temporally. However, they stressed that the ecological phenomenon under consideration may be better studied by an explicit, simultaneous consideration of spatial and temporal variation.

Studies examining both spatial and temporal components of variation are numerous, including a broad range of disciplines (e.g., community ecology, soil sciences, plant physiology, systematic biology, population ecology, and agricultural science). The approaches used to examine spatial and temporal variation are almost as diverse. All too often, however, qualitative methods are employed in which the variable(s) under consideration, or their coefficient of variation (CV), are simply plotted against time and (or) space. Subjective analyses are subsequently made regarding aspects of this variation (e.g., see Yoshiyama et al. 1986; Luk et al. 1989; Lara-Lara et al. 1990; Hubert and O'Shea 1991; Post et al. 1995).

To introduce some quantitative aspects, Horwitz (1978) examined the temporal variability in stream discharge and noted that about half of the regressions of the CV (ln flow) against stream position were significantly negative, indicating a pattern of reduced temporal variability in flow downstream. Lewis (1978), noting that spatial and temporal variation are rarely considered simultaneously in plankton studies, presented a more quantitative method of examination through the use of a two-way random-effects analysis of variance (ANOVA). The sum of squares from the species abundance matrix was partitioned into spatial, temporal, interaction (ephemeral), and error components for each individual species. The component sums of squares were subsequently converted to variance components. However, these variance components were compared in a subjective manner by plotting ratios of them against one another to show the relative importance of the spatial and temporal components. This method has been employed in studies such as Threlkeld (1983), Urabe (1989), Matthews (1990), and Meador and Matthews (1992). Although the method was more quantitative than other approaches, it was univariate and the comparison of the variation components was ultimately still qualitative.

ANOVAs have been commonly employed to test for differences among variables over time or space (e.g., see Wright 1989; Moore and Reis 1983; Stang and Hubert 1984; Helmissaari and Siltala 1989; Oyama 1990), as has Kendall's coefficient of concordance to test for consistency in species abundance rankings across time or space (e.g., see Matthews 1990; Rahel 1990; Houle 1994). Examples of ANOVAs being applied to similarity matrix values also exist (Matthews et al. 1988; Matthews 1990), a process that violates the assumptions underlying the ANOVA F test (e.g., statistical independence of the values).

The complex nature of community data has been a catalyst for the rapid development and transfer of multivariate methods in ecology. Ordination techniques, designed to summarize and simplify large data sets, can help to elucidate factors contributing to the structure of the community under consideration (Ludwig and Reynolds 1988). However, examples of multivariate approaches examining spatial and temporal variation are sparse. Karr et al. (1987) followed the changes in the multivariate, yet arbitrarily defined, index of biotic integrity over time and space in two Mississippi River and one Lake Erie drainage streams. Evans (1988), in studying prairie grasshopper communities in relation to periodic fires, followed the movement of 30 time-site points in multivariate space, concluding that their pattern was sufficiently restricted as compared with that of a random walk model to term the community dynamics predictable. Mahalanobis distance was used to compare between-month differences in phytoplankton assemblages by Peterson and Stevenson (1989). Gelwick (1990) used an ANOVA on ordination axis scores of sites ordinated spatially and temporally to test for significant patterns.

Our review is by no means intended to be exhaustive, but rather simply to serve to highlight some important points. Many of these traditional approaches to the study of spatial and temporal variation can be criticized as suffering from some or all of the following problems: (*i*) partially or wholly qualitative in nature; (*ii*) of limited scope as univariate methods are employed (i.e., covariation is ignored); (*iii*) subjective in their interpretations; (*iv*) failing to formally test the underlying

structure or distribution of the variation. To examine the structure and organization of communities, a quantitative, multivariate, and objective technique that reveals the underlying structure and distribution of the spatial and temporal variation is required.

The primary purpose of this study is to introduce and demonstrate the use of a new multivariate method for the examination and testing of the structure of the variation within a data set, both spatially and temporally. An intuitive, graphical technique for partitioning the variation in multivariate space is presented. Through the use of hypothesis matrices constructed to partition the variation in specific patterns, statistical assessment of the distribution of the variation can be explored through the use of principal coordinates analysis and Mantel's test. This method is demonstrated using a data set of littoral-zone fish community abundances from three lakes in south-central Ontario over three sampling periods.

Secondly, the varying influence of different similarity measures is explored. Numerous measures of similarity (and distance) exist in the ecological literature. These measures often stress different aspects of the data and the choice of which measure to use is commonly a subjective aspect of data analysis. The influence of different ordination methods on the results obtained is a similar and well-documented phenomenon (Kenkel and Orlóci 1986; Minchin 1987; Jackson 1993*b*). Thus, principal coordinates analysis is performed using three of the common similarity measures in the ecological literature (Euclidean distance, Bray–Curtis measure, and Pearson product-moment correlation coefficient) and the results are compared.

Quantitative results, such as are obtained with this method, can be used to explore the structure and organization of aquatic communities. There are few studies that examine both the spatial and temporal patterns of variation in freshwater fish communities in general, and specifically those found in the littoral zones of lakes (e.g., Hinch and Collins 1993; Hinch et al. 1994; Pierce et al. 1994). By revealing the spatial and (or) temporal scales at which significant variation occurs in the community, this method creates a more informative picture than a homogenization of the data over larger scales. Mechanistic explanations of the causes of the variation may be possible through detailed analysis focused at the scale at which the variation occurs. Specifically our approach may be used to identify the relative importance of spatial and temporal components, thereby allowing proper experimental design for testing various community-related questions.

Results from this method allow a number of questions affecting the structure of the variation in aquatic communities to be examined. These questions include the following. (*i*) Does the structure of the community vary over time? If so, how? (*ii*) Does it vary among lakes? (*iii*) Does it vary within a lake? (*iv*) Do any of these components dominate the variation in the community? With an understanding of questions such as these, the larger and perhaps more important issue of why spatial and temporal variation exists in aquatic communities can be addressed. The identification of pattern is the principal step that must be taken to answer such a question. To reiterate Resh and Rosenberg (1989, p. 941), ". . . it is this spatial and temporal variability that often provides an explanation of factors causing the patterns observed."

Fig. 1. Location of the study lakes in south-central Ontario, with maps of the three lakes. Depth contours are in metres; sampling sites are indicated by the numbered circles.
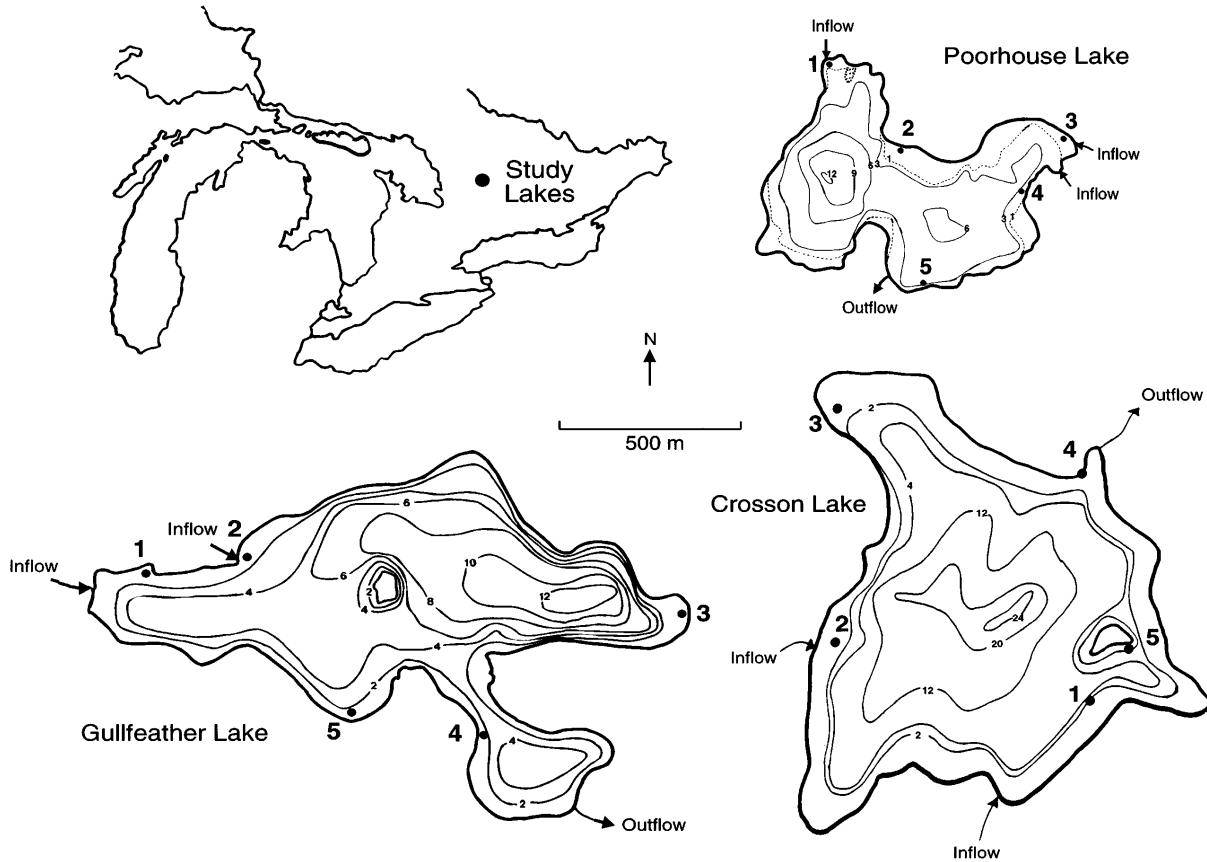

Table1. Attributes of the study lakes.

	Crosson	Gullfeather	Poorhouse
Latitude	45°05′	45°06′	45°22′
Longitude	79°02′	79°01′	78°45′
Area (ha)	56.8	68.9	30.2
Maximum depth (m)	23.5	13.0	13.1
Mean depth (m)	8.4	4.8	4.1
Surface area (ha)	56.8	68.9	30.2
pH	5.91	5.51	6.90
Conductivity (µS/cm)	23.7	24.5	42.0
Secchi depth (m)	3.2	2.0	3.1

Methods

Data collection

Gullfeather, Crosson, and Poorhouse lakes are softwater lakes (Table 1) located in south-central Ontario (Fig.1). Five littoral zone sites in each lake (Fig. 1) were trapped for two 24-h intervals during each of three sampling periods. The three sampling periods were during the first weeks of June, July, and August of 1994. Sites were chosen arbitrarily to represent the range of different littoral- zone habitats in each lake. One plastic (Casselman and Harvey 1973) and two standard minnow traps (baited with dog kibble) per site were set at approximate depths of 1 m. In each 24-h period the fish were collected, identified, and released. The total catch of both gears for the 2 consecutive nights formed the abundance value for each site. A total of 9789 fish from 15 species were caught in the three lakes over the three sampling periods (Table 2). With the exception of the cool-

water white sucker *Catostomus commersoni* and brook trout *Salvelinus fontinalis*, all the species can be characterized as warm-water species. A data matrix of 45 sites (5 sites per lake × 3 lakes × 3 sampling periods), as defined by their total species catches, was created. All species were used in the subsequent analysis.

Data analysis

Principal coordinates analysis (Gower 1966; Legendre and Legendre 1983; Digby and Kempton 1987) was performed on the total species abundance data set. Sites were ordinated to maximize the amount of variance summarized in a minimum number of axes. Principal coordinates analysis (PCoA) was performed using three different similarity measures: Euclidean distance, Bray–Curtis measure, and Pearson product-moment correlation coefficient (Ludwig and Reynolds 1988; Krebs 1989). These measures were chosen to represent commonly used similarity measures in the ecological literature.

Lake- and sampling-period centroids were calculated as the geometric centres of their respective groups of points on each ordination. For instance, the Poorhouse Lake centroid was placed on the ordination as the average PCoA score for the 15 Poorhouse Lake sites (5 sites/sampling period × 3 sampling periods) for each axis. The sampling-period centroids were calculated as the average score on each axis of the 15 points during any one sampling period (5 sites/lake × 3 lakes), irrespective of their lake membership. Lake-time centroids were calculated as the mean PCoA score for each axis of specific lake-time combinations. Thus, these centroids represent the mean scores of only five points on the ordination.

Variance was calculated using the mean of the squared deviation from the mean. Inherent in a PCoA is the centring of the data such that the average PCoA score for all of the points on each axis is zero. Thus, the mean of the first two PCoA axes is represented by the origin (0,0)

2170

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

Table 2. Total catch summed over all sites in a lake during a sampling period.

Scientific name	Common name	Crosson Lake			Gullfeather Lake			Poorhouse Lake		
		Sampling period 1	Sampling period 2	Sampling period 3	Sampling period 1	Sampling period 2	Sampling period 3	Sampling period 1	Sampling period 2	Sampling period 3
Lepomis gibbosus	Pumpkinseed	140	192	240	90	192	116	189	159	233
Micropterus salmoides	Largemouth bass	0	0	0	0	2	1	0	0	0
Notemigonus crysoleucas	Golden shiner	181	725	475	59	68	72	141	280	91
Notropis cornutus	Common shiner	0	0	0	0	0	5	54	0	4
Semotilus atromaculatus	Creek chub	4	14	27	1	1	6	181	124	152
Chrosomus eos	Northern redbelly dace	24	18	23	0	0	0	201	269	208
Semotilus margarita	Pearl dace	0	0	0	0	0	0	434	682	492
Rhinichthys atratulus	Blacknose dace	0	0	0	0	0	0	16	2	11
Pimephales notatus	Bluntnose minnow	8	1	1	0	0	0	651	786	738
Pimephales promelas	Fathead minnow	0	0	0	0	0	0	93	291	276
Perca flavescens	Yellow perch	50	45	44	35	15	16	0	0	0
Ictalurus nebulosus	Brown bullhead	62	6	3	0	0	0	4	15	31
Catostomus commersoni	White sucker	0	3	0	1	1	6	0	0	1
Culaea inconstans	Brook stickleback	0	0	0	0	0	0	2	1	0
Salvelinus fontinalis	Brook trout	0	0	0	0	0	0		4	0

Note: Sampling period 1, June; sampling period 2, July; sampling period 3, August.

Fig. 2. Example of the actual Bray–Curtis distance matrix (sampling period 1) and the corresponding model or null matrix constructed for use in a Mantel test. The model matrix was constructed to test the hypothesis that all of the variation is among lakes (spatial) with complete similarity within a lake. Only the first three of the five sites per lake are shown for clarity of presentation.
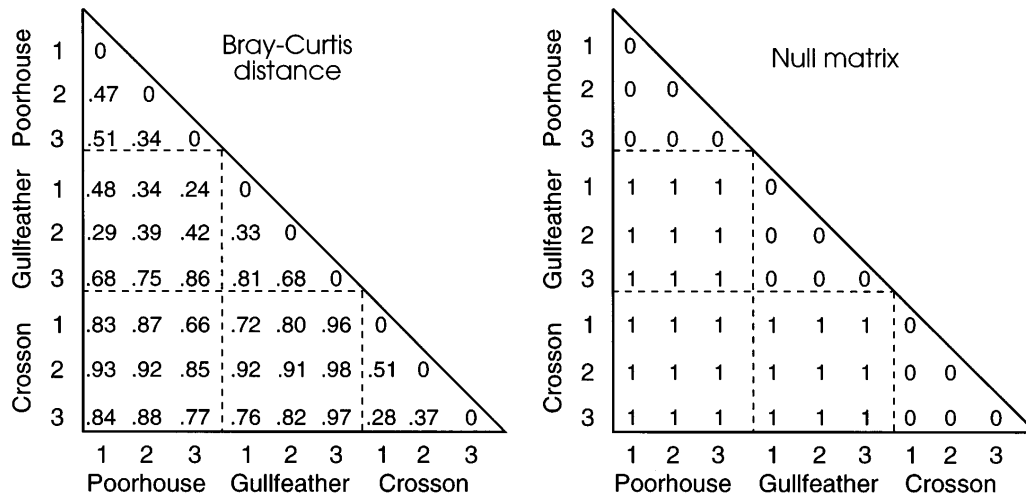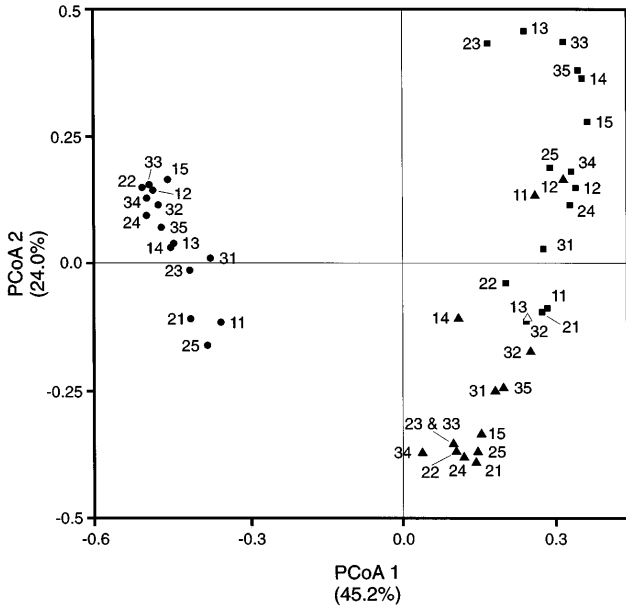

on a two-dimensional plot. The squared deviations of points from the mean represent a measure of dispersion with more deviant points being more heavily weighted. The sum of these distances represents a measure of variation. The total variation in the reduced, multivariate data set was calculated as the sum of the squared distance from the origin to each point. This total variation was then partitioned into the various within- and among-centroid components, e.g., among-lake and among-time components of variation in community composition.

A Mantel test (Mantel 1967; Jackson and Somers 1989) was used to assess whether individual components of variation relative to the total differed from random. Using an approach similar to that of Schnell et al. (1985), matrices were artificially constructed to reflect the specific hypothesis in question. Distance matrices (similarity matrices in the case of Pearson's correlation coefficient) were constructed of 1's and 0's. For instance, a distance matrix to test whether the community data showed a nonrandom pattern in among-lake variation would have 0's in all of the within-lake comparisons (indicating no intralake distance) and 1's in all of the among-lake comparisons of sites (indicating differences) (Fig. 2). Mantel's Z, measuring the degree of association between the distance and hypothesis matrices, was calculated and compared with a null distribution of test statistics as generated by 10 000 permutations of one of the matrices (Jackson and Somers 1989). The significance of association was indicated by the proportion of permuted Z statistics that was as large as or more

Fig. 3. Principal coordinates analysis of abundance data using Bray–Curtis measure. Numerical codes represent sampling period (1, June; 2, July; and 3, August) followed by site number within the specified lake. Points represent Poorhouse Lake (●), Crosson Lake (▲), and Gullfeather Lake (■).

Table 3. Spearman's rank correlation of the original species abundances with the first two PCoA axes scores obtained using the Bray–Curtis measure.

	PCoA 1	PCoA 2
Bluntnose minnow	−0.85	0.10
Northern redbelly dace	−0.83	0.13
Pearl dace	−0.82	0.16
Fathead minnow	−0.82	0.15
Creek chub	−0.81	−0.17
Blacknose dace	−0.62	0.17
Brown bullhead	−0.34	−0.13
Golden shiner	−0.31	−0.95
Brook stickleback	−0.27	−0.03
Pumpkinseed	−0.17	−0.44
Brook trout	−0.13	−0.02
Common shiner	−0.12	0.27
Largemouth bass	0.14	0.34
White sucker	0.23	0.31
Yellow perch	0.58	−0.39

Note: Significance levels are not presented because the axes are not statistically independent of the species abundances.

Fig. 4. Principal coordinates analysis of abundance data using Bray–Curtis measure. Stars represent lake centroids. Variation accounted for by lake membership is represented by the squared distance of a centroid from the origin (heavy solid lines). Distance from individual points to their respective centroids (dotted, dashed, and light solid lines) represents residual variation not accounted for by lake membership. Lake symbols as in Fig. 3.

extreme than the observed *Z* statistic. Similarity matrices derived from Pearson's product-moment correlation coefficient were transformed from a –1 to +1 range to a 0 to +2 range by adding 1 to every value. This was necessary as positive and negative values present in a matrix could in effect cancel one another out and give a nonsignificant *Z* statistic with strongly structured matrices.
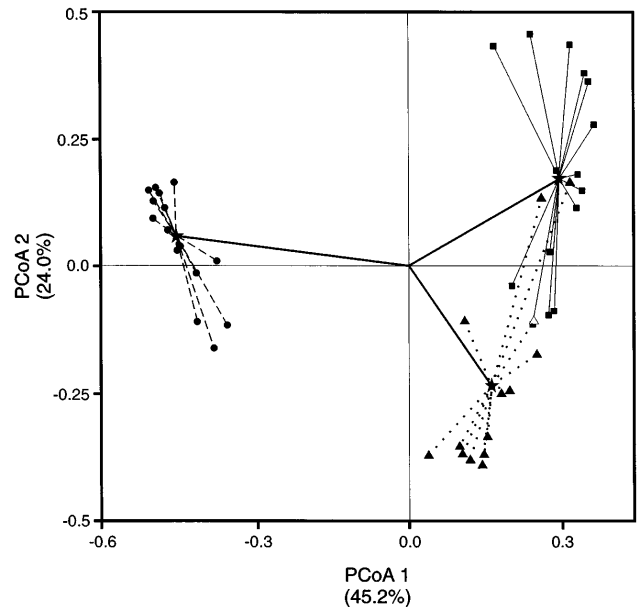
Results

The first two components extracted using PCoA with the Bray–Curtis measure accounted for a greater proportion of the variance (65.2%) than that expected under a broken-stick model (Jackson 1993*a*). Poorhouse Lake separated from Crosson and Gullfeather lakes along the first component (Fig. 3). The first component contrasted sites with high abundance of bluntnose minnow, creek chub, northern redbelly dace, pearl dace, and fathead minnow from sites with zero or low abundance of these species (Table 3). Crosson and Gullfeather lakes separated less distinctly along the second component, which primarily contrasted sites on the basis of golden shiner abundance (Table 3). The squared length of a line joining a lake centroid to the origin represents the amount of the overall variation that can be explained by the shared spatial (lake) component of those sites forming the centroid and the degree of deviation of those sites from the sites in the other lakes (Fig. 4). The average squared length of the lines joining the individual sites to their respective lake centroids represents the average amount of variation that is unaccounted for by the spatial (lake) membership of a site. These amounts, the sum of the squared distances from the centroids to the origin and the average squared distance from the sites to their respective centroids, are presented in Table 4 as percentages of the total variation under the rows for totals in the lake and residuals categories, respectively.
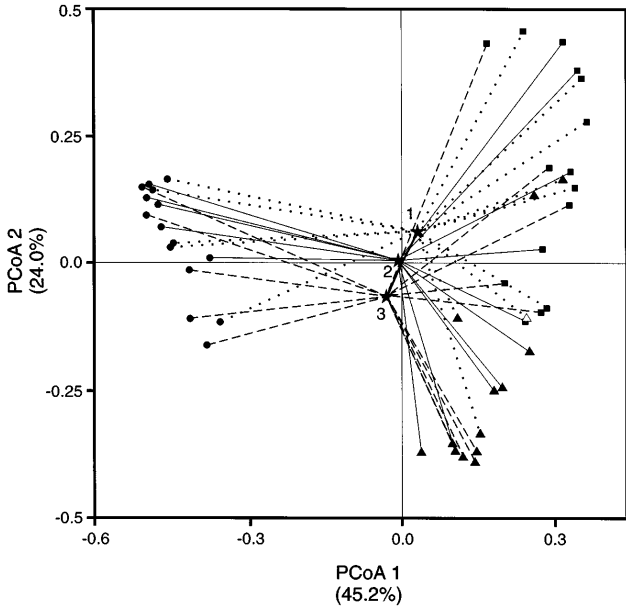
An identical procedure was conducted using the same ordination (except with the sampling period centroids) to examine the temporal variation. The squared distance from the origin to a centroid represents the amount of variation for a member site owing to the time when the site was sampled (Fig. 5). Approximately 3% of the total variation was attributable to the sampling periods (Table 5). Most of this was during sampling periods 1 and 2 whereas virtually no variation could

2172

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

Table 4. Partitioning of the spatial variation.

Variation component		Similarity coefficients		
		Euclidean distance	Bray–Curtis measure	Correlation coefficient
Lake	Total	66.9	81.2	75.7
	Crosson	21.8	20.0	23.0
	Gullfeather	19.2	28.8	23.1
	Poorhouse	59.0	51.2	53.9
Residuals (within lake)	Total	33.1	18.8	24.3
	Crosson	25.8	39.6	34.3
	Gullfeather	1.9	46.4	49.5
	Poorhouse	72.3	14.0	16.2

Note: Lake component represents the variation accounted for by the lake membership of samples. Residuals represent variation unaccounted for by the lake membership of samples. Totals (lake and residuals) are percentages of the total variation in the data set (and thus sum to 100). Values for individual lakes represent their contribution to their respective total.

Table 5. Partitioning of the temporal variation.

Variation component		Similarity coefficients		
		Euclidean distance	Bray–Curtis measure	Correlation coefficient
Sampling period	Total	3.2	3.0	1.3
	Crosson	43.4	49.3	39.5
	Gullfeather	55.8	50.5	58.4
	Poorhouse	0.9	0.2	2.1
Residuals (within periods)	Total	96.8	97.0	98.7
	Crosson	20.1	32.5	31.6
	Gullfeather	46.0	32.1	34.6
	Poorhouse	33.9	35.4	33.9

Note: Sampling period component represents the variation accounted for by the time of sampling of a site. Residuals represent variation unaccounted for by the time of sampling. Totals (lake and residuals) are percentages of the total variation in the data set (and thus sum to 100). Values for individual sampling periods represent their contribution to their respective totals.

Fig. 5. Principal coordinates analysis of abundance data using Bray–Curtis measure. Stars represent sampling period centroids as indicated by numbers. Variation accounted for by time of sampling is represented by the squared distance of a centroid from the origin (heavy solid lines). Average squared distance from individual points to their respective centroids (dotted, dashed, and light solid lines) represents residual variation not accounted for by the time of sampling. Lake symbols as in Fig. 3.

Fig. 6. Principal coordinates analysis of abundance data using Bray–Curtis measure. Stars represent specific lake-time centroids; numbers indicate sampling times. Variation accounted for by lake membership and the time of sampling of a site is represented by the squared distance of its centroid from the origin (heavy solid lines). Average squared distance from individual points to their respective centroids (dotted, dashed, and light solid lines) represents residual variation not accounted for by the lake-time membership of a point. Lake symbols as in Fig. 3.

be attributed to the temporal component of period 3. The remaining variation (i.e., approximately 97%) was of a non-temporal nature. The average squared distance from the individual sites to their respective centroid represents the amount of variation within the sampling period, i.e., the amount of variation not accounted for by the time of sampling of a site.
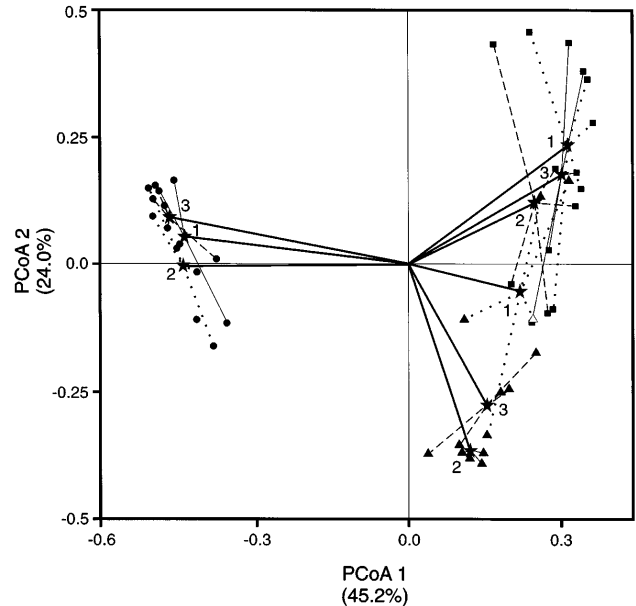
Interactions between time and the lakes were analysed by an analogous procedure, each centroid being defined by a specific lake and time combination (Fig. 6). The squared distance

of the centroids from the origin represents site-specific temporal variation. It is the amount of variation accounted for by the lake and time of sampling of a site. Site-specific temporal variation is somewhat analogous to the interaction term of an ANOVA, namely it can demonstrate when the difference between the levels of one main effect (lake) depends on the level of the other main effect (i.e., time). Between 73 and 86% of the variation in the communities is accounted for by this

Table 6. Partitioning of the variation among time-site combinations.

Variation component		Similarity coefficients		
		Euclidean distance	Bray–Curtis measure	Correlation coefficient
Lake by time	Total	73.7	86.1	79.7
	C1	4.4	3.8	4.7
	C2	14.8	11.9	12.8
	C3	7.0	7.8	8.4
	G1	6.1	12.0	7.3
	G2	5.6	6.1	8.0
	G3	5.8	9.7	6.8
	P1	10.8	15.5	17.5
	P2	27.5	15.5	15.8
	P3	18.2	17.7	18.8
Residuals (within lake by time)	Total	26.3	13.9	20.3
	C1	3.2	19.2	16.5
	C2	2.1	0.3	3.9
	C3	9.2	5.4	5.1
	G1	0.8	18.5	19.8
	G2	0.8	18.8	18.3
	G3	0.8	21.6	20.5
	P1	15.9	6.0	3.9
	P2	39.0	8.0	5.9
	P3	28.4	2.3	6.2

Note: Lake-by-time component represents the variation accounted for by the time and lake of sampling. Residuals represent variation unaccounted for by the time and lake of sampling. Totals (lake-by-time, residuals) are percentages of the total variation (and thus sum to 100). Values for individual lake-site combinations represent their contribution to their respective totals. Cod are ln; G, , Poorwed by sampling time.

temporal–spatial interaction (Table 6). This indicates that species composition varied among the sites over time, but that the change in the pattern was not consistent across the sites.

PCoA ordinations using Pearson's correlation coefficient (Fig. 7) and Euclidean distance measure (Fig. 8) were analysed by procedures analogous to those performed with the Bray–Curtis measure (Tables 4–6). The Euclidean distance measure stressed the absolute differences in abundance in the Poorhouse sites more than the other measures, resulting in these sites being spread out along the first axis. The total spatial component was thus lower than when using the other measures (Table 4). This effect is also observed in Tables 4 and 6 as an elevated Poorhouse Lake contribution to the residual variations. The ordination resulting from Pearson's correlation coefficient (Fig. 7) resembled that of the Bray–Curtis measure (Fig. 3) with the exception that the second axis was reversed.

The hypothesis matrix structuring all of the variation among the lakes, with complete similarity within a lake, showed significant association with all three of the observed similarity matrices for all three sampling periods ($p < 0.001$ in all cases, see Table 7). The hypothesis matrix structuring all the variation among time, with complete similarity within a time, differed in its results depending on the lake. Gullfeather and Poorhouse lakes showed nonsignificant associations whereas Crosson Lake showed a significant association (Table 7). The probabilities ranged as high as 0.19, depending on the similarity measure used.

Fig. 7. Principal coordinates analysis of abundance data using Pearson's correlation coefficient. Lake symbols as in Fig. 3.
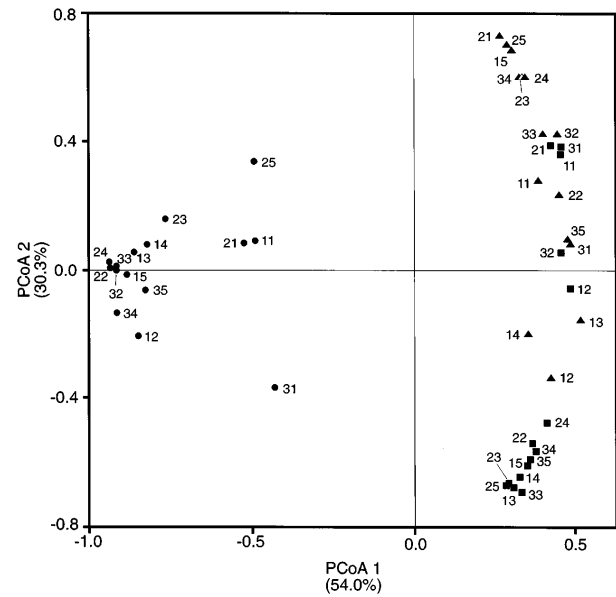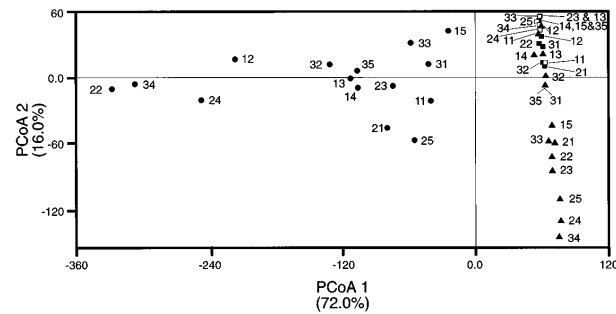

Fig. 8. Principal coordinates analysis of abundance data using Euclidean distance. Lake symbols as in Fig. 3.

Discussion

Evaluating the new approach

This method of partitioning the variation has a number of advantages over other approaches. It is quantitative, yielding percentages of the variation accounted for by the spatial and temporal components. Its multivariate nature allows large, complex data sets to be examined without arbitrarily eliminating information (e.g., species of lower abundances are often eliminated from analyses using ANOVAs). The multivariate approach also allows the community to be examined as a unit, removing the necessity to subdivide it into its individual component species. This retains patterns of covariation between species that are lost in univariate approaches. The use of centroids is not restrictive in its application. The distribution of the variation at different temporal and spatial scales could be examined, as could the structure of variation using any group defined a priori. Different measures of community resemblance can also be used to accommodate different types of data (e.g., presence–absence, ordinal, or continuous) as well as permitting different attributes (e.g., relative versus absolute abundance) to be emphasized.

2174

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

Table 7. Probabilities from Mantel's test of observing a result equal to or more extreme than that derived from a comparison of the similarity matrices with hypothetical matrices of the structure of the variation.

	All variation among lakes[a]			All variation among times[b]		
Similarity coefficient	Sampling period 1	Sampling period 2	Sampling period 3	Crosson	Gullfeather	Poorhouse
Euclidean distance	0.0002	0.0001	0.0001	0.0099	0.7047	0.7477
Bray–Curtis measure	0.0001	0.0001	0.0001	0.0011	0.6430	0.6427
Correlation coefficient	0.0007	0.0001	0.0001	0.0437	0.8359	0.5596

[a]Hypothesis matrix with all of the variation distributed among the lakes and complete similarity within a lake (e.g., Fig. 2).

[b]Hypothesis matrix with all of the variation distributed among the sampling periods and complete similarity within any sampling period.

Testing for significant patterns through the use of Mantel's test is an important aspect. Most ordination analyses are not hypothesis-testing procedures, but are simply methods of summarizing and displaying large, complex data sets. Interpretation of ordinations is often based upon the assumption that nonrandom patterns exist, resulting in the overinterpretation of some ordinations lacking such patterns (Jackson et al. 1992; Jackson 1993a). The construction of hypothesis matrices of the distribution of the variation for use in Mantel's tests provides statistical evaluation of the observed ordination patterns, thus eliminating some of the subjectiveness.

Comparisons of the results for the partitioning of the variation using the similarity measures (Tables 4–6) highlight a subjective aspect of ordination techniques. The results depend on the similarity measure used. In more general terms, the choice of ordination methods (e.g., principal components analysis, correspondence analysis, PCoA) influences the results (Kenkel and Orlóci 1986; Minchin 1987; Jackson 1993b). PCoA was chosen as it allows the exploration of the varying influences of different commonly used similarity measures. Different measures of resemblance may lead to different interpretations of the significance relative to the hypothesis matrix (Table 7). Morista's index partitioned the variation in a similar manner to the correlation coefficient, and results using the Canberra metric were similar to the Bray–Curtis measure (H.D. Rundle, unpublished results). A point to be stressed is that the structure of the variation does not exist in absolute terms but rather is a product of how it is defined and measured. However, by including a number of similarity measures in the analysis, concordance of results strengthens the interpretation (Green 1979).

Euclidean distance is strongly influenced by absolute differences in species' abundances. Thus, the contribution of the individual lakes to the lake and residual spatial variation (Table 4) follows the order of the total lake abundances. Poorhouse Lake, with the highest total catch, accounts for the largest percentage of both the lake and residual components. Crosson Lake is intermediate in its total abundance and likewise in the proportion of the total for which it accounts. Gullfeather Lake, with consistently low species abundances, contributes the least to both totals. This pattern is not seen with the other two measures. Euclidean does not separate Gullfeather and Crosson lakes in the ordination to the same degree as the other measures because of the lower abundances of fish in these two lakes. The points on the Poorhouse Lake ordination, with its high abundances, are spread out much more. Thus, the high and varying abundances in Poorhouse Lake increase its contribution to the residual component (Table 4) and also increase the total residual value. This effect

is not observed with the correlation coefficient nor with the Bray–Curtis measure.

The Bray–Curtis measure ignores joint absences and is thus dominated by the more abundant species. This is seen in the ordination by the tighter clusters within a lake, resulting in the largest total of all of the measures in the lake component (Table 4). Pearson's correlation coefficient, being relatively insensitive to proportional or additive changes in abundances, also forms tighter clusters than those formed using Euclidean distance.

Interpreting patterns in littoral-zone fish communities

Studies examining the spatial and temporal variation in littoral-zone fish communities are rare. Examples to date have examined a limited range of spatial or temporal scales that are chosen arbitrarily. Data are often pooled across spatial and temporal scales that are not of interest, independent of any knowledge as to the structure of the variation. Such a homogenization may reveal broad patterns that are more easily interpreted, but if the patterns do not represent the scales at which variation dominates, any mechanistic explanation is incomplete. Pierce et al. (1994) demonstrated significant lake, lake-by-year, lake-by-season, and year-by-season effects in an ANOVA on the total fish biomass of 10 southern Quebec lakes, but then pooled the data for each lake to examine the relationship between multivariate ordinations of the fish community, limnological variables, and prey community. Other work has focused on multi-lake comparisons that attempt to identify variables whose association with fish abundance stands out against a background of variation (i.e., Hinch and Collins 1993). To examine interlake and interyear models of fish community abundance, Hinch and Collins (1993) used data collected only during May and June of each year in an attempt to reduce seasonal variation. Without knowledge of the structure of the variation, one cannot assess whether the interyear variation is confounded by temporal variation on shorter scales, or even whether it is the largest source of variation in these communities.

The clear separation of the three lakes in multivariate space, using all three similarity measures, indicates three communities differing substantially in their composition and abundance of constituent fishes. Distinct separation of lakes in ordination space was also noted by Hinch et al. (1991, 1994) and Pierce et al. (1994). The clear separation of the lakes with little tendency of clumping into similar community types may result when geographic separation of the lakes is limited (Pierce et al. 1994). It may also result when the presence or absence of different species strongly influences the ordination. The correlations of the species with PCoA 1, when compared with the

species abundances (Tables 2–3), show that species presence or absence strongly influences the ordination. PCoA 1 contrasted lakes on the basis of the presence (Poorhouse Lake) and absence or near absence (Gullfeather and Crosson lakes) of bluntnose minnow, pearl dace, and fathead minnow. Abundances of creek chub and northern redbelly dace showed similar patterns. The strong influence of species presence or absence was also noted by Hinch et al. (1991), despite efforts to remove it by only including the species that occurred in ≥60% of the lakes.

Explanations for the observed community patterns require exploration through studies of the interaction of the species with limnological, predator, prey, and other variables. Past research suggests a number of possibilities. Pierce et al. (1994) found only one significant correlation, that between total fish biomass and chironomid biomass. No significant correlations were found with any of their limnological or prey variables. Hinch et al. (1994) demonstrated a significant correlation between lake elevation and abundance, while Hinch and Collins (1993) demonstrated significant correlations between *Lepomis* biomass and lake primary productivity, nearshore macrophyte cover, and lake flushing rate in different groups of lakes. Associations with any of these variables, or others, could potentially explain our observed patterns. However, as our study is based on three lakes, comparisons of results against lake physical and chemical conditions are not very informative. Given knowledge of the structure of the variation, any explanation must be able to encompass the spatial and temporal patterns observed. Interestingly, the pattern of species richness in our results does not demonstrate the commonly observed positive correlation with lake surface area (i.e., Pierce et al. 1994). Poorhouse Lake, the smallest but most nutrient-rich lake, is the most species rich whereas the largest lake (Gullfeather) has the fewest species.

Along with the multivariate differences in the structure and composition of these fish communities, a number of general similarities can be identified regarding how the variation is structured. A significant spatial component was identified in the littoral-zone fish communities. By simply knowing only the lake from which a catch was taken, one can account for approximately 67–81% of the variation in community composition. The temporal component is a nonsignificant factor in community variation in Gullfeather and Poorhouse lakes but a significant factor in Crosson Lake. By knowing only the time of sampling of any site, little information is gained as approximately 97–99% of the variation remains unaccounted. When comparing Tables 4 and 6, one notes only small increases in the total variation when the lake and time of sampling are known relative to knowing the lake alone. The 67–81% range increases to approximately 74–86%. The residual component of the variation is within-lake variation at a specific time. This is variation at the site level, as each lake and sampling time combination represented the average of five sites within a lake.

Results indicate that the variation within the multivariate structure of these littoral zone communities is largely due to among-lake differences. The among-lake variation is significantly greater than the within-lake and temporal variation. Pierce et al. (1994) found similar results for their 10 study lakes where an ANOVA testing for lake effects on the total biomass of the 8 most common species indicated highly significant results.

Crosson Lake stands out from the others owing to the additional presence of a small but significant temporal component in its variation. The existence of a temporal component in only one lake again stresses the importance of the spatial aspect. The time of sampling did not have an effect as a whole but was important within one lake. Pierce et al. (1994) found no significant seasonal aspect to the total biomass of their eight most common species when pooled across their 10 study lakes. Seasonal results were indicated for some of the individual species (i.e., yellow perch and pumpkinseed). However, their study only examined two sampling periods (early and late summer) and pooled the data across 10 lakes, thus losing the information on the individual lakes. Total biomass plots of all species for each lake demonstrated much variation between early and late summer in their study lakes. Our results indicate that pooling such as this can obscure among-lakes differences.

Crosson Lake differs in this manner primarily because of the temporal pattern of golden shiner abundance. The second PCoA axis was negatively correlated with golden shiner abundance (Table 3). Golden shiner was the most abundant species in Crosson Lake and it showed large changes over the three sampling periods (Table 2). A similar pattern of golden shiner abundance peaking during sampling period 2 was observed in Poorhouse Lake. Explanations for this temporal pattern require exploration at the species level. Possibilities include the nature of recruitment and its interaction with certain lake attributes and (or) the other species present. However, multiyear studies are required to assess such recruitment-related possibilities.

Finally, the scale of this study must not be overlooked (Hinch 1991). The temporal variation represented variation within one season and these results do not preclude significant variation among seasons: the spatial variation was at the whole-lake level, leaving both smaller and larger scales to be explored. Once the data are collected, the statistical method presented for examining the structure of the variation is easily applied to larger or longer scales.

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2176

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

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