

## Multiscale spatial distribution of a littoral fish community in relation to environmental variables

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### Abstract

Using a new statistical tool, Principal Coordinates of Neighbor Matrices, we decomposed the signals representing the variation of fish community composition, fish density, and biomass in the littoral zone of a lake to assess the relative contributions of a series of spatial scales to the overall signal. We also quantified the relationship between variations of fish community descriptors and environmental conditions at different spatial scales. The fish community exhibited scale-dependent variability that we grouped into four categories at spatial scales ranging from 2 km (very broad scale) to <100 m (fine scale). These scales were associated with specific environmental variables, suggesting the presence of scale-dependent ecological processes within the lake. Following the hierarchy theory, we propose that Lake Drouin was primarily structured by the fetch, a very broad scale physical process. Through energy inputs, fetch might have influenced the appearance of various physical structures (i.e., rocky substrates, woody debris, and macrophyte beds) at finer spatial scales (i.e., broad and meso). Functional groups of species were observed and classified according to the range of spatial scales to which they were associated. Cyprinids and small-sized species displayed a multiscale spatial distribution, whereas the distribution patterns of zoobenthivores were restricted to a single spatial scale. This study provides quantitative support to the idea that the littoral zone of lakes can be perceived as a hierarchical arrangement of habitats that differ not only by the environmental conditions among them but also by the spatial scales at which environmental conditions vary within them.

Littoral zones represent the most diversified, productive, and heterogeneous portions of lakes (Wetzel 1990). They are characterized by a diversity of microhabitats composed of a variety of physical and biological structures that result in complex biological interactions (Werner et al. 1977). Fish communities of the littoral zone are thus commonly exposed to a structurally complex environment over multiple spatial scales, ranging from millimeters (e.g., foliage structure of macrophytes) to hundreds of meters (e.g., distance between weed beds or tributaries; Weaver et al. 1997). Consequently, the interactions between littoral fish communities and their habitats can take place at different spatial scales. Hence, both the abiotic and biotic factors observable at different spatial scales could influence the structure of fish communities.

The word “scale” commonly has been used in various contexts and with multiple meanings (Gozlan et al. 1998; Thompson et al. 2001). Dungan et al. (2002) provided a framework to define scale in ecology. According to these authors, the spatial scale of a study can be related to three specific concepts: observation (sampling) scale, scale of spatial analysis, and scale of ecological phenomena. In this study, the word scale is used in terms of the scale of spatial analysis.

The spatial scale at which a study is conducted has a great

influence on the perceived effect of environmental factors on fish community descriptors. It is expected that the relative importance of a suite of environmental variables explaining the variation of descriptors of fish communities might vary with the spatial scale at which observations are made (Syms 1995). This is essentially related to the expectation that community descriptors observed at any given scale could be the result of processes occurring at different spatial scales (Imhof et al. 1996). Moreover, the hierarchical theory predicts that complex systems, such as lakes, are generated by intertwined ecological processes that are hierarchically structured (Allen and Starr 1982). Ecological processes occurring at finer spatial scales are the products of interacting multiple causes generated at broader spatial scales. Thus, the development of relationships between community descriptors and environmental conditions across a wide range of spatial scales represents a stepping stone in the understanding of scale-dependent ecological processes (Wiens 1976; Menge and Olson 1990).

Mathematical approaches are increasingly used to study the distribution of fish at multiple spatial scales (Poizat and Pont 1996; Bult et al. 1998; Wilson 2001). By identifying relationships between fish community descriptors and environmental conditions on a spectrum of spatial scales, these approaches can be thought of as reflecting the perception an organism might have of its environment, rather than the perception of the investigator. Consequently, these approaches not only enhance comprehension of the structure of fish communities, they also improve our assessment of fish habitat requirements (Bult et al. 1998). Borcard and Legendre (2002) and Borcard et al. (2004) have recently developed a statistical method, Principal Coordinates of Neighbor Matrices (PCNM), which can be used to describe the dominant spatial scales at which species are varying. In comparison to

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### Acknowledgments

We thank M. Coignon and J. Guimmond-Cataford for valuable field assistance. The nonparametric multivariate analysis of variance program used in the Web Appendix was kindly provided by Marti J. Anderson, Department of Statistics, University of Auckland.

Financial support was provided by scholarships from NSERC and FQRNT to A.B.'A., by an NSERC research fund to D.B. and P.L. (OGP7738), and as FQRNT-Team to D.B. and P.L.

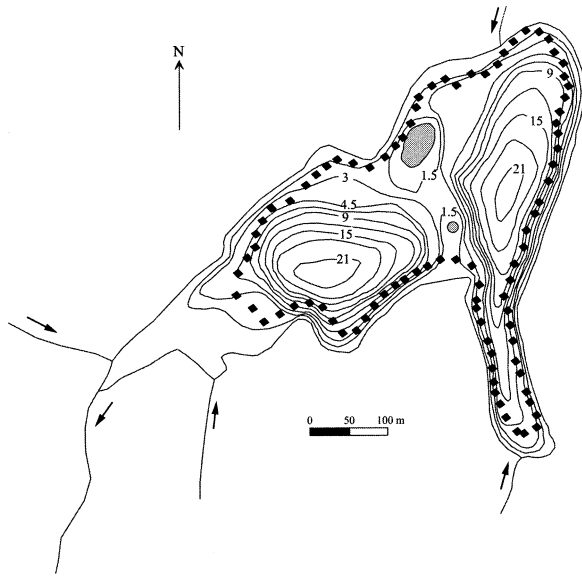


Fig. 1. Map of Lake Drouin (Lanaudière, Québec). Black diamonds represent the 90 sampling sites in the littoral zone of the lake. Depths are given in meters.

other multiscale approaches that operate at a few selected scales, this method presents the advantage of analyzing a wide range of spatial scales. The PCNM method is based on the spectral decomposition of a survey space into a complete series of spatial scales under a spatially continuous sampling design.

In this study, we used the method of Borcard and Legendre (2002) and Borcard et al. (2004) to investigate the multiscale distribution of a fish community in a lake located on the Laurentian shield in Québec, Canada. We specifically tested four hypotheses: (1) the variance of the littoral zone fish community can be decomposed into fractions of variance corresponding to different spatial scales; (2) the structure of fish communities perceived at different spatial scales can be related to environmental variables that vary at these scales; (3) the spatial scales at which a fish community is structured, as well as the explanatory potential of environmental variables, can vary within a season; and (4) the species can be classified from generalists to specialists according to the range of spatial scales at which they vary the most.

## Methods

**Study lake**—Sampling was conducted in Lake Drouin (46°09'W, 73°55'N; Lanaudière region of Québec, Canada) during spring and summer 2001 (Fig. 1). Lake Drouin was selected for this study because it has a diversified littoral zone with woody debris, rocky substrate, sandy beaches, and patches of macrophytes of mixed species, such as the water shield *Brassenia schreberi*, pipewort *Eriocaulon aquaticum*, Eurasian milfoil *Myriophyllum spicatum*, and water lilies *Nymphaea* sp. This mesotrophic lake has a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km (calculations based on the sum of the size of each sampling unit). The water column is thermally stratified from May to

October. During this period, surface water temperature ranges from 15°C to 26°C and bottom temperature from 4°C to 8°C. The thermocline forms at 4.5 m depth in mid-June and breaks down in early October.

**Sampling procedure**—A series of fish community descriptors and physical variables were quantified over 90 sites that covered the complete perimeter of the study lake. The length of a sampling site was defined by its shore length; the mean length was 53.9 m (range 40.6–67.2 m). The width of a sampling site (5–10 m) was determined by the distance from the shore to the 3 m depth isobath. The limit of 3 m was adopted because it corresponded to the depth at which all fish observed could be correctly counted and identified to the species level while snorkeling. The mean width of a site was 10.5 m (range 9–12 m). Geographical coordinates were estimated at each site by a global positioning system (Garmin-GPS 12) with a precision of  $\pm 10$  m. The perimeter of the lake was further separated into two sections comprising 48 (Section 1) and 42 sites (Section 2). These sections were surveyed for 2 d consecutively (i.e., Section 1 was sampled during day 1 and Section 2 was sampled during day 2). This procedure was used because a maximum of 50 sites could be surveyed within 4–5 h. Sampling was limited to this time interval each day because local fish community composition can change among periods within a day (dawn, midday, dusk; Keast and Harker 1977). The sites were surveyed three times (i.e., on 6 consecutive days) in the spring (from 25 to 30 June), and again during the summer (from 29 July to 4 August). The sites from the 2 consecutive days (i.e., two sections) were put in the same data file, representing the complete perimeter of the lake as a circular continuum. The data for the three pairs of days (i.e., three complete perimeters) were then added within homologous sections of the lake. This addition of the sections was done to minimize the effects of daily variations of fish community characteristics at each site. The justification for this procedure is given in Web Appendix 1 at [http://www.aslo.org/lo/toc/vol50/issue\\_2/0465al.pdf](http://www.aslo.org/lo/toc/vol50/issue_2/0465al.pdf).

**Fish community sampling**—The fish community was surveyed with a modified version of the visual survey technique described by Harmelin-Vivien et al. (1985). This technique requires two observers that snorkel at the water surface, performing zigzags over the complete length and width of a sampling site, following a trajectory globally parallel to the shore. During the surveys, the distance between the two observers was kept to  $\sim 4$  m. This technique allowed the observers to cover 90% of the total area of each site. The observers maintained a constant swimming speed of 10 m  $\text{min}^{-1}$  to minimize fish disturbance (Eklöv 1997). The snorkelers noted their observations on plastic polyvinyl chloride cylinders. They identified the species, their relative abundances, and the approximate sizes of the fish (Table 1) as they progressed along the transect. The relative abundance of fish was noted in six classes: 1 = 1 individual, 2 = 2 individuals, 3 = 3 individuals, 4 = 4 or 5 individuals, 5 = 6–9 individuals, and 6 = 10 individuals or more. Table 1 shows the species size classification that was used during the surveys.

Table 1. Species size classes used in the text. The species marked with an asterisk was excluded from the analysis because its total abundance was <1%. Numbers in parentheses indicate the percentage (%) of fish observed by size class.

Species	Code	Size (mm)	
		Small	Large
<i>Pimephales promelas</i> (fathead minnow)	Pipr*	≤40	41–90
<i>Perca flavescens</i> (yellow perch)	Pefl	55–109(65)	110–230(35)
<i>Lepomis gibbosus</i> (pumpkinseed)	Legi	30–109(95)	110–195(5)
<i>Ameiurus nebulosus</i> (brown bullhead)	Amne	50–109(25)	110–190(75)
<i>Notemigonus crysoleucas</i> (golden shiner)	Nocr	65–109(64)	110–225(36)
<i>Semotilus atromaculatus</i> (creek chub)	Seat	55–69 (55)	70–135(45)
<i>Catostomus commersoni</i> (white sucker)	Caco	55–159(41)	160–320(59)
<i>Fundulus diaphanus</i> (banded killifish)	Fudi	55–64 (77)	65–85 (23)

Brind'Amour and Boisclair (2004) recently compared visual surveys to seine catches for a set of community descriptors. They found that most of the descriptors obtained by visual surveys were estimated with an accuracy similar to that of seining. The total fish density and relative fish biomass were underestimated during visual surveys. However, both descriptors showed similar patterns across the different habitats in lakes. This study suggested that mapping the spatial distribution of total fish density and relative fish biomass with visual surveys on the basis of the approach described above might be appropriate when these descriptors vary at least twofold among the sampling sites.

Table 2. Numerical resolutions and codes for the environmental variables observed at each site.

Environmental factor	Code	Numerical resolution
Average littoral slope	Lit	Quantitative
Average depth (m)	Z	Quantitative
Average temperature	Temp	Quantitative
Average dissolved oxygen	O <sub>2</sub>	Quantitative
Substrata		
Sand (<2 mm)	S1	Presence/absence
Gravel (2–60 mm)	S2	Presence/absence
Rock (60–250 mm)	S3	Presence/absence
Boulder (>250 mm)	S4	Presence/absence
Bedrock	S5	Presence/absence
Woody debris	S8	Presence/absence
Riparian use		
Cottage/brick wall	U1	Presence/absence
Forest	U2	Presence/absence
Beach	U3	Presence/absence
Bush	U4	Presence/absence
Wharf	U5	Presence/absence
Riparian trees	Tree	Presence/absence
Macrophytes		
Average density of emergent	Emer	Quantitative
Average density of submersed	Sub	Quantitative
Percent cover	Cov	Percentage
Riparian slope	Riv	Presence/absence
Fetch (m)	Fet	Quantitative
Tributary	Trib	Presence/absence

*Computations*—The fish community at each site was characterized with three types of descriptors: community composition, total fish density, and relative fish biomass. Total fish density was calculated by dividing total fish abundance by the unit area of the sampling site. Because the abundance data ( $n_i$ ) obtained during the visual surveys were collected in classes, we transformed them into abundance values as follows: 1 = 1 individual, 2 = 2 individuals, 3 = 3 individuals, 4 = 5 individuals, 5 = 8 individuals, and 6 = 10 individuals. This change of state of the abundance data from ordinal to quantitative allowed us to compute the community descriptors. The relative fish biomass ( $B$ ) for any combination of species and size class was estimated as

$$B = \sum n_{i,s} \times W_{i,s} \quad (1)$$

where  $n_{i,s}$  is the number of fish per species per size class and  $W_{i,s}$  is the average fish mass (g) per species per size class estimated with the length–mass relationships published in Schneider et al. (2000) and from relationships estimated in our laboratory for Laurentian lakes (Comeau and Boisclair unpubl.).

*Environmental variables*—Sampling sites were characterized by measuring 11 environmental variables at each site: average temperature (°C), dissolved oxygen (mg L<sup>-1</sup>), average littoral slope (m), average water depth (m), substrate composition (nominal: sand, gravel, rocks, boulders, bedrock, woody debris), riparian use (nominal: cottage, forest, beach, bush, wharf), density of macrophytes (described following, emergent, submersed, bottom cover), riparian slope (presence/absence), riparian trees (presence/absence), fetch (described following), and tributary (presence/absence; Table 2). All environmental variables, with the exception of average temperature, dissolved oxygen, density of macrophytes, and fetch, were noted during a pilot study at the end of May 2001. The temperature, dissolved oxygen, and fetch were estimated on each sampling day. Fetch was defined as the effective distance to the nearest shore in the direction of the predominant wind. The density of macrophytes at each site was estimated once per survey period by two snorkelers in four randomly selected 1-m<sup>2</sup> quadrats (a 1-m<sup>2</sup> frame was thrown from the center of the sampling site in different directions within each site). The number of stems from emer-

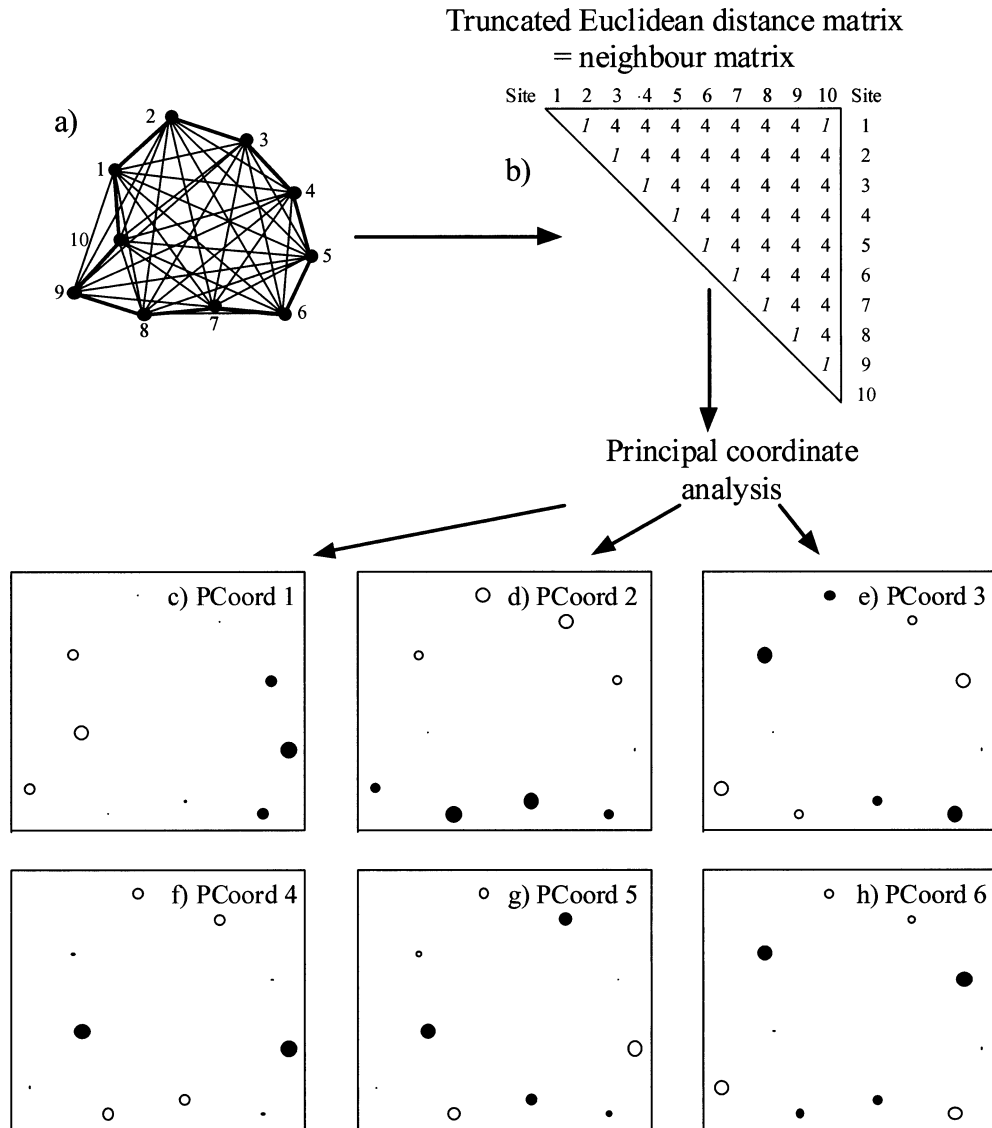


Fig. 2. PCNM variables around a fictitious structure forming a loop. (a) Sites localized on the map. (b) Neighbor matrix. Distances between neighboring sites (heavy lines in panel a) are written in the neighbor matrix in panel b; these distances are equal to 1 in the example. Distances between nonadjacent sites (light lines in panel a) are replaced by four times the maximum value (max = 1 in the example,  $4 \times \text{max} = 4$ ). (e–h) The successive PCNMs are presented by bubbles on the map of the sites: positive values are filled; negative values are empty.

gent and submersed species per 1 m<sup>2</sup> was counted. The average number of stems from the four replicates was used in the statistical analysis. The percent cover of plants covering the substrate, representing a tight carpet of *M. spicatum*, was estimated.

**Statistical analyses**—Multiscale patterns: Spatial patterns over a wide range of scales were detected and quantified with the PCNM method proposed by Borcard and Legendre (2002) and Borcard et al. (2004). Using the geographical coordinates of our sampling sites, we constructed a matrix of Euclidean distances among the sites. We truncated the matrix to retain the distances between neighboring sites. The distances larger than a threshold value, chosen to be the larg-

est distance between the centers of two contiguous sites, were replaced by an arbitrarily very large value equal to four times that threshold. For instance, the largest distance between two contiguous sites in our study was 100 m. We replaced all the values of nonneighboring sites with a value equal to 400 ( $4 \times 100$  m). The distance between the first and last site was also retained to form a closed loop that depicts the natural structure of a lake shore (Fig. 2). The choice of that arbitrary value was made according to a sensitivity analysis done by Borcard and Legendre (2002). They found that multiple regressions that used principal coordinates obtained with a multiplicative constant of four and above yielded the same  $R^2$  and the same  $p$  values as with any other multiplicative constant larger than four. We com-

puted a principal coordinate analysis of the truncated distance matrix and kept only the coordinates corresponding to positive eigenvalues. The resulting 60 principal coordinates (called principal coordinates of neighbor matrices) were used as explanatory variables either in canonical redundancy analyses (RDA; Rao 1964), computed for the community composition transformed with the Hellinger transformation proposed by Legendre and Gallagher (2001), or in multiple regressions in the case of global metrics (total fish density and relative fish biomass). Significant PCNMs were identified by either (1) a forward selection procedure in the program CANOCO (ter Braak and Smilauer 1998) with unrestricted permutations for the community composition (multiple response variables) or (2) a multiple regression with forward selection of the explanatory variables in SPSS (1999) for the global metrics (single response variable).

PCNM variables correspond to a series of sinusoids with decreasing periods. On the basis of the similarity of their periods, the significant PCNMs were grouped into submodels. These submodels are linear combinations of the significant PCNMs pertaining to a given scale. Only the submodels of significant PCNMs associated with the first canonical axis were analyzed. The second canonical axis was either not significant or represented <5% of the total variability of the fish community.

Species abundance data: An RDA was calculated with the species matrix as the response data and each spatial PCNM submodel, in turn, as the explanatory variable. The loadings of the species scores from the RDA provided the contributions of the species to each spatial submodel.

Environmental variables: A multiple regression analysis with forward selection was carried out with the use of SPSS (1999). The environmental variables were used to explain the submodels describing the spatial distributions of the fish community descriptors (i.e., community composition, total fish density, and relative fish biomass) at each spatial scale. The threshold probabilities for the partial  $F$  statistics used in the selection were  $p = 0.05$  to include and  $p = 0.10$  to remove a variable.

## Results

A total of 10,500 fish belonging to eight species were observed in the 90 sites visually surveyed in our study. Of these fish, 59% were observed in June, whereas 41% were observed in August. *Lepomis gibbosus* (L.) represented 51% of the total number of fish observed. Six species each represented <20% of the total number of fish: *Notemigonus crysoleucas* (M.), *Semotilus atromaculatus* (M.), *Fundulus diaphanus* (L.), *Ameiurus nebulosus* (L.), *Perca flavescens* (M.), and *Catostomus commersoni* (L.).

The community composition, total fish density, and relative fish biomass varied greatly between sampling sites in June (Fig. 3a) and August (Fig. 3b). An exception was observed in *L. gibbosus* (Legi), which displayed high densities in almost all the sites in the 2 sampling months. The other species, as well as the total fish density and the relative fish

biomass, were distributed in patches of varying sizes localized in different regions of the lake.

*Classification of spatial scales*—The variance of the littoral fish community was decomposed with respect to submodels of significant PCNMs. On the basis of the similarity of their periods, the PCNMs were grouped into four submodels: a very broad scale submodel with a range of nearly 2 km, corresponding to PCNM 1 and 2; a broad-scale submodel ranging from 500 to 1,000 m, corresponding to PCNMs 3–9; a mesoscale submodel ranging from 200 to 450 m, which corresponded to PCNMs 10–35; a fine-scale submodel with a range of <100 m corresponding to PCNMs 36–60.

*Multiscale patterns*—June: The three descriptors of the fish community displayed spatial variability across 19 of the 60 PCNMs (Table 3). These principal coordinates accounted for 20%, 42%, and 46% of the among-site variability of community composition, of total fish density, and of relative fish biomass, respectively. The PCNMs were grouped into four submodels, ranging from very broad to fine scale.

Only *N. crysoleucas* (Nocr) varied significantly at a very broad spatial scale (Table 4a). The density of *N. crysoleucas* was highest in the northern part of the lake (Table 5a; Fig. 4a). The environmental variables explained 51% of the spatial variation in density of *N. crysoleucas* (Table 6). Fetch (Fet) was the explanatory variable contributing most to the model, as shown by its standardized coefficients ( $b = 0.565$ ). Four other explanatory variables contributed to the model at that scale: density of emergent macrophytes (Emer), bottom cover (Cov), presence of riparian forest (U2), and the presence of woody debris (S8).

Only *S. atromaculatus* (Seat) was correlated to the broad-scale model (Table 4a). The density of *S. atromaculatus* was highest on the northern shore of the lake and on the western shore of the bay (Table 5a; Fig. 5a). Total fish density and relative fish biomass reached their highest values at the tip of the elongated bay in the southern portion of the lake, along the northeastern shore and on the west side of the lake (Table 5a; Fig. 5b). The environmental variables that significantly contributed to the broad-scale submodels were similar among the community descriptors (Table 6); they explained 26%, 17%, and 36% of the among-site variability in community composition, total fish density, and relative fish biomass, respectively. Littoral slope (Lit  $b = -0.376$ ) was the variable contributing most to the community composition submodel. The presence of woody debris (S8  $b = 0.279$ ) and the riparian slope (Riv  $b = -0.409$ ) were the environmental variables contributing most to the total fish density and relative fish biomass submodels. Other variables related to the type of substrate (sand S1, boulders S4) also contributed to the three submodels.

At meso scale, the three types of community descriptors displayed spatial dependency. Two different spatial distribution patterns were observed (Fig. 6a,b). The first distribution pattern, displayed by community composition, consisted of patches of three species, *N. crysoleucas* (Nocr), *S. atromaculatus* (Seat), and *C. commersoni* (Caco; Fig. 6a), that alternated with those of *L. gibbosus* (Legi) and *F. dia-*

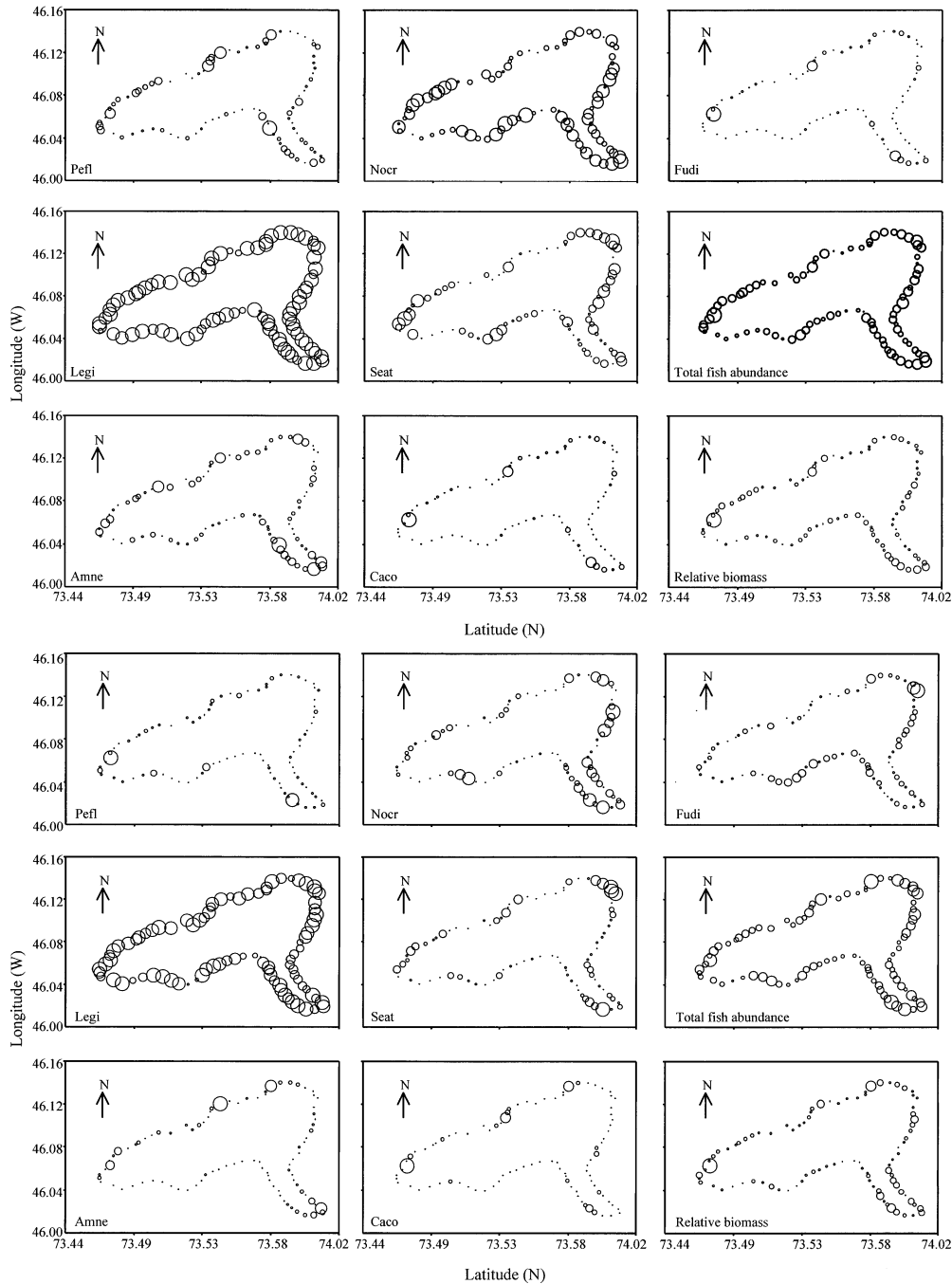


Fig. 3. Map of Lake Drouin showing the observed values of the fish community descriptors for the months of (a) June and (b) August. The size of the bubbles is proportional to the observed values.

*phanus* (Fudi; Table 5a). The second pattern showed patches of high forecasted values of total fish density and relative fish biomass. These two descriptors reached their highest values in patches at the tip of the elongated bay, on the southeastern part of the lake, and along the northwestern shore (Table 5a; Fig. 6b). The environmental variables (Table 6) explained 20% of the community composition, 30% of the variance of relative fish biomass, and a rather small proportion (5%) of the variability in total fish density. The bot-

tom cover by macrophytes ( $\text{Cov } b = 0.304, b = -0.371$ ) contributed most to the community composition and relative fish biomass submodels. The fetch (Fet) and the emergent macrophytes (Emer) also contributed to the community composition and relative fish biomass submodels. The presence of tributary (Trib) and presence of riparian forest (U2) were the two other variables associated with the meso submodel of relative fish biomass. Total fish density was only associated with riparian trees ( $\text{Tree } b = -0.217$ ).

Table 3. Regression/canonical coefficients for standardized variables of fish community descriptors detected at different spatial scales in June. Column headings include coefficients of determination ( $R^2$ ) for the whole spatial model.

PCNM no.	Community composition ( $R^2=0.195$ )	Total fish density ( $R^2=0.422$ )	Relative fish biomass ( $R^2=0.455$ )	Spatial scale
1	-0.138			Very broad
3	0.169	-0.240	-0.216	Broad
4	0.518		0.230	Broad
5	0.199	-0.314	-0.215	Broad
6	-0.231			Broad
7	-0.353	0.269		Broad
10	0.165	-0.216	0.299	Meso
11	0.257			Meso
13	-0.341	0.284	0.200	Meso
14			-0.165	Meso
15		0.258		Meso
18	-0.229			Meso
19	-0.132			Meso
26	-0.181			Meso
36	-0.265			Fine
44	0.289			Fine
47			-0.192	Fine
58	0.024		0.266	Fine
60			-0.213	Fine

Only the PCNM submodels for the community composition and relative fish biomass displayed spatial dependency at fine scale. They showed similar spatial distributions within the lake; patches of high abundance and relative fish biomass estimates were regularly distributed along the shore (Fig. 7a; Table 5a). The species scores showed that *P. flavescens* (Pefl), *A. nebulosus* (Amne), *F. diaphanus* (Fudi), and *S. atromaculatus* (Seat) were distributed in small patches, <100 m long and fairly regularly spaced along the shore of the lake. The density of the four species was not explained by any environmental variable (Table 6), whereas the presence of tributary (Trib  $b = -0.228$ ) contributed a small amount to the relative fish biomass model at that scale ( $R^2 = 0.052$ ).

August: The three community descriptors displayed patterns of spatial variability similar to that in June, across 24 of the 60 PCNM variables (Table 7). These principal coordinates accounted for 23%, 48%, and 46% of the community composition, total fish density, and relative fish biomass, respectively. The PCNMs were grouped into four submodels, ranging from the very broad to fine scale.

Similar patterns of spatial variability of community composition, total fish density, and relative fish biomass were observed at very broad scale (Fig. 4b; Table 5b). Species scores indicated that *L. gibbosus* (Legi) was more abundant along the eastern part of the lake (Table 4). The abundance of *N. crysoleucas* (Nocr) showed the inverse distribution pattern, being most abundant in the western part of the lake. Total fish density and relative fish biomass values were more abundant in the western part of the lake (Fig. 4b). High proportions of the variability of community descriptors were explained by the environmental variables (Table 8; com-

Table 4. Species scores on the first canonical axis of each spatial scale submodel for the months of June and August. See Table 1 for the species codes. No significant relationship was found between the community composition and the fine spatial scale in August.

	Very broad	Broad	Meso	Fine
June				
Pefl	-0.149	0.275	0.035	-0.227*
Legi	-0.066	0.284	-0.374*	-0.019
Amne	0.167	0.279	-0.008	-0.223*
Nocr	0.258*	-0.283	0.237*	-0.020
Seat	0.031	-0.499*	0.372*	0.284*
Caco	-0.065	0.241	0.319*	0.072
Fudi	-0.164	-0.029	-0.276*	-0.229*
August				
Pefl	-0.165	-0.312*	-0.002	
Legi	-0.260*	0.142	-0.364*	
Amne	0.081	-0.335*	-0.021	
Nocr	0.377*	-0.259*	0.421*	
Seat	0.116	-0.289*	0.438*	
Caco	0.008	-0.138	0.100	
Fudi	0.096	0.377*	-0.240	

\* Species that markedly contribute to a given scale.

munity composition 72%; total fish density 76%; relative fish biomass 76%). Fetch (Fet) was the environmental variable that contributed most to the three very broad scale submodels ( $b = -0.749$ ;  $b = -0.802$ ;  $b = -0.802$ ). The abundance per species was explained by three other environmental variables that contributed to the submodel: the

Table 5. Median values of the fish community descriptors for the four submodels for the months of June and August. See Table 1 for the species codes.

	Very broad	Broad	Meso	Fine
a) June (fish m <sup>-2</sup> )				
Pefl				0.001
Legi			0.024	
Amne				0.001
Nocr	0.009		0.008	
Seat		0.012	0.001	0.003
Caco			0.000	
Fudi			0.003	
Total fish density		0.086	0.078	0.001
Relative fish biomass (g m <sup>-2</sup> )		2.061	1.707	1.698
b) August (fish m <sup>-2</sup> )				
Pefl		0.000		
Legi	0.025		0.025	
Amne		0.000		
Nocr	0.008	0.004	0.001	
Seat		0.001	0.002	
Caco				
Fudi		0.002		
Total fish density	0.078	0.079	0.082	0.088
Relative fish biomass (g m <sup>-2</sup> )	0.923	0.942	0.923	0.733

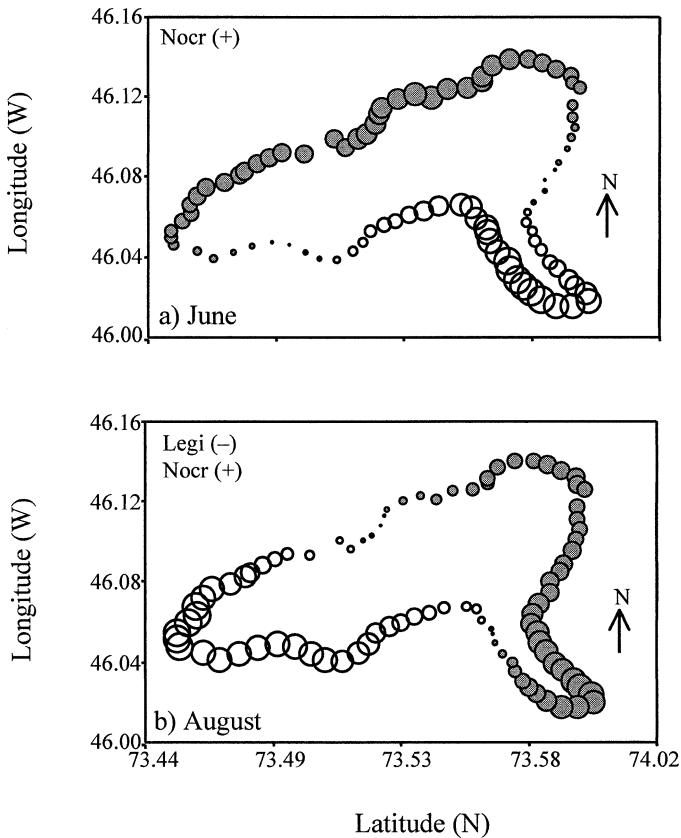


Fig. 4. Map of Lake Drouin showing (a) the forecasted values of the community composition in June and (b) the three fish community descriptors in August at the very broad scale ( $\geq 2$  km). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (-) are abundant in the filled and empty bubbles, respectively; see Table 4 for details. Species codes are given in Table 1.

density of emergent macrophytes (Emer), bottom cover by macrophytes (Cov), and presence of riparian trees (Tree). The total fish density and total biomass submodels were explained by the same environmental variables: the presence of riparian trees (Tree), density of emergent macrophytes (Emer), riparian slope (Riv), and sand as substrate (S1).

Similar patterns of spatial variability of community composition, total fish density, and relative fish biomass were observed at broad scale in August (Table 7). Four species were distributed along the northern and southern parts of the lake (Table 4b; Fig. 5c): *P. flavescens* (Pefl), *A. nebulosus* (Amne), *N. crysoleucas* (Nocr), and *S. atromaculatus* (Seat). *F. diaphanus* (Fudi; Table 5b) was mostly found at the tip of the elongated bay and on the western part of the lake. Total fish density and relative fish biomass displayed the same abundance pattern as *F. diaphanus*. The environmental variables explained 14%, 29%, and 33% of the spatial variation of the community composition, total fish density, and relative fish biomass (Table 8). At that scale, the percent contribution of boulders to the substrate (S4) was the environmental variable that contributed most to all submodels ( $b = -0.373$ ,  $b = -0.420$ ,  $b = -0.536$ ). Woody debris (S8) was the other variable that contributed to the total fish den-

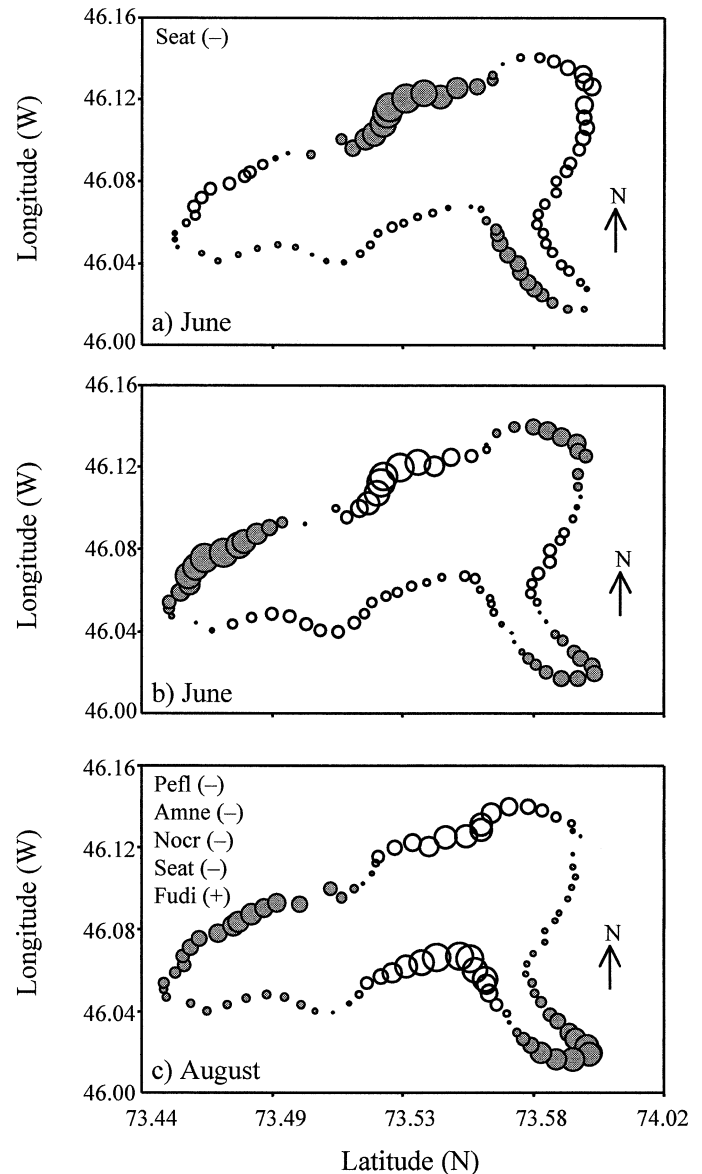


Fig. 5. Map of Lake Drouin showing (a) the forecasted values of the community composition and the total fish density and (b) relative fish biomass in June. (c) The community composition, the relative fish biomass, and the total fish density in August at the broad scale (500–1,000 m). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (-) are abundant in the filled and empty bubbles, respectively; see Table 4 for details. Species codes are given in Table 1.

sity model, whereas rock as substrate (S3), the presence of riparian trees (Tree), and bottom cover by macrophytes (Cov) contributed to the relative fish biomass submodel.

At meso scale, the community descriptors displayed a pattern of variation consisting patches ranging from 100 to 500 m along the shore (Fig. 6c; Table 5b). The species scores indicated that *L. gibbosus* (Legi) and *N. crysoleucas* (Nocr) were both distributed inversely with *S. atromaculatus* (Seat). Only the PCNM submodels for the community composition (13%) and relative fish biomass (15%) could be explained by environmental variables at that scale (Table 8). The sub-



Table 6. June standardized coefficients ( $b$ ) of environmental variables that explained significant components of the spatial patterns (PCNM models) of the littoral fish community descriptors at four spatial scales. See Table 2 for the environmental variable codes. Column headings include coefficients of determination ( $R^2$ ) of the models.

	Community composition			Total fish density		Relative fish biomass		
	Very broad ( $R^2=0.513^{***}$ )	Broad ( $R^2=0.263^{***}$ )	Meso ( $R^2=0.198^{***}$ )	Broad ( $R^2=0.171^{***}$ )	Meso ( $R^2=0.047^*$ )	Broad ( $R^2=0.363^*$ )	Meso ( $R^2=0.295^*$ )	Fine ( $R^2=0.052^*$ )
Riv		-0.247**		-0.211*		-0.409***		
Lit		-0.376***						
Z								
S1		-0.214*				-0.226*		
S3								
S4				-0.220*		-0.353***		
S5								
S8	-0.167*			0.279**				
U1								
U2	0.195*						0.193*	
U3								
U4								
U5								
Tree					-0.217*			
Sub								
Emer	0.325***		-0.292**				0.195*	
Cov	0.232**		0.304**				-0.371***	
Fet	0.565***		0.262*				-0.292**	
Trib							0.315***	-0.228*

\*  $0.01 < p \leq 0.005$ ; \*\*  $0.001 < p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ .

model of the relative fish biomass was explained by the presence of riparian trees (Tree  $b = 0.389$ ). Bottom cover by macrophytes (Cov  $b = 0.266$ ) and riparian trees (Tree  $b = -0.208$ ) contributed to explain a significant portion of the variability in community composition.

At fine scale, only the total fish density and relative fish biomass displayed significant submodels (Fig. 7b; Table 5b). A fairly small proportion of the total variability in fish density (5%) was explained by the presence of a beach (U3  $b = 0.217$ ), whereas none of the measured environmental variables explained the relative fish biomass submodel (Table 8).

## Discussion

The spatial components explained, on average, 37.5% of the fish community variability in Lake Drouin. The littoral fish community displayed spatial dependency at multiple spatial scales. These scales were grouped into four categories characterized by several spatial ranges, including a very broad scale (nearly 2,000 m), a broad scale (from 500 to 1,000 m), a meso scale (from 200 to 450 m), and a fine scale (<100 m). Following the hierarchy theory of Allen and Starr (1982), our study suggests that Lake Drouin could be primarily structured by fetch, a very broad scale physical process. Through energy inputs, fetch could have influenced the appearance of various physical structures (i.e., rocky substrates, woody debris, and macrophyte beds) at finer spatial scales (i.e., broad and meso). These spatially structured habitats (Table 9) in turn influence the littoral fish community,

likely causing scale-dependent ecological processes to appear within the lake. The influence of spatially-structured habitats on fish community have been observed for coral reef communities (Gust et al. 2001; Wilson 2001) and rivers (Pozizat and Pont 1996; Lohr and Fausch 1997). However, to our knowledge, no other study has shown that littoral fish communities within lakes are also structured over multiple spatial scales. This is mainly because most of the within-lake studies concentrate on fine-scale habitat partitioning, addressing questions related to competition or other species interactions, therefore restricting the sampling effort to a limited range of abiotic factors (Jackson et al. 2001). Because our study covered the complete perimeter of the littoral zone at a fine-scale sampling unit (~50 m), we were able to relate fish community variation to a broad range of environmental variables.

*Spatially structured habitats*—At the very broad scale, fetch ( $b = 0.57$ – $0.75$ ) and, to a lesser extent, emergent macrophytes ( $b = 0.28$ – $0.33$ ) were the most important variables describing the habitat for the fish community. Fetch is commonly used to provide a measure of site exposure, and exposure can influence the fish community in several ways. According to Nixon (1988) and Randall et al. (1996), fish production ( $\text{kg ha}^{-1}$ ) and fish abundance might be positively correlated to mechanical energy provided by the wind. The distribution and composition of sediments depends notably on physical processes (e.g., wave action and wind) which redistribute them in different parts of lakes (Cyr 1998). Suspended sediments can, in turn, determine the distribution and

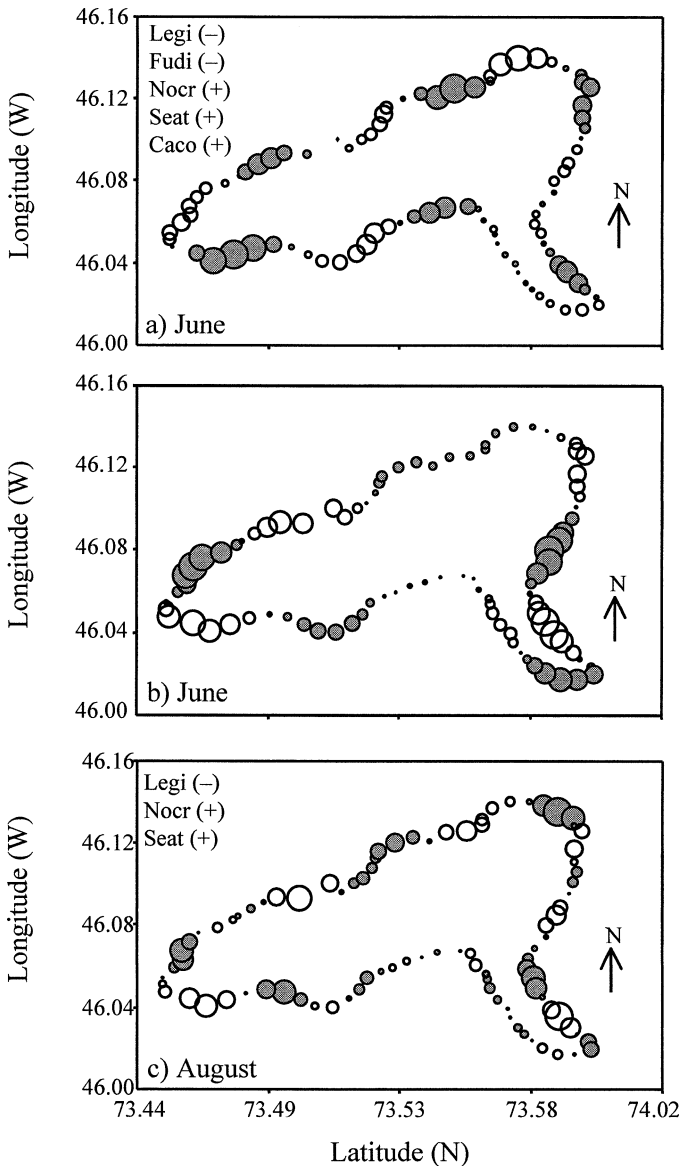


Fig. 6. Map of Lake Drouin showing (a) the forecasted values of the community composition and the total fish density and (b) relative fish biomass in June. (c) The three fish community descriptors in August at the meso scale (300–500 m). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (-) are abundant in the filled and empty bubbles, respectively; see Table 4 for details. Species codes are given in Table 1.

biomass of benthic organisms (Burkholder 1992), which might provide food resources for the fish. Fetch might also indirectly affect macrophyte growth, which in turn can procure refuges to certain fish species. Intermediate fetch has a positive effect on macrophyte growth (Keddy 1983) and, as several studies have shown, macrophytes positively affect the density of littoral fish within a lake (Hinch and Collins 1993). In our study, fetch and emergent macrophytes were not correlated. They were, however, always associated with the same spatial scales (very broad and meso) in both months. Because we sampled the macrophytes and the fetch

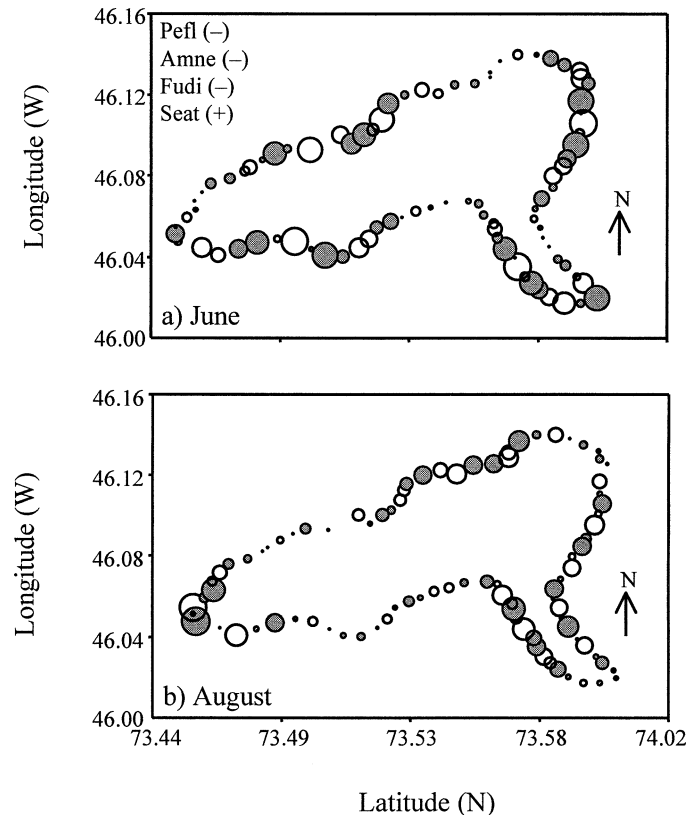


Fig. 7. Map of Lake Drouin showing (a) the forecasted values of the community composition and the relative fish biomass in June. (b) The total fish density and the relative fish biomass in August at the fine scale (<100 m). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (-) are abundant in the filled and empty bubbles, respectively; see Table 4 for details. Species codes are given in Table 1.

on only two occasions within each season, we might not have covered a sufficient temporal scale to observe a potential positive relationship.

Habitats at broad scale (500–1,000 m) were composed of heterogeneous physical substrates ranging from rocks and boulders ( $b = 0.21$ – $0.54$ ) to woody debris ( $b = 0.28$ ) and low littoral slopes. Studies in lakes with limited growth of macrophytes have shown that rocky and woody substrates have the same ecological importance as macrophytes in structuring fish communities (Beauchamp et al. 1994; Falcon et al. 1996). Interstices between rocks serve as refuges from predation for small fish and benthic species (Beauchamp et al. 1994). According to Aumen et al. (1990), woody debris and coarse rocky substrates positively affect nutrient recycling by providing suitable substrates for colonization by heterotrophic microorganisms and algae, thereby procuring food resources to fish.

Habitats described at the meso scale included organic bottom, macrophytes, and riparian trees. However, only low proportions of the variability of the community descriptors were explained by these environmental variables at that scale ( $R^2 = 0.05$ – $0.30$ ). The influence of wooded riparian zones on fish communities has received much attention in stream ecosystems (Collares-Pereira et al. 1995; Jones et al. 1999).

Table 7. Regression/canonical coefficients for standardized variables of fish community descriptors detected at different spatial scales in August. Column headings include coefficients of determination ( $R^2$ ) for the whole spatial model.

PCNM no.	Community composition ( $R^2=0.231$ )	Total fish abundance ( $R^2=0.483$ )	Relative fish biomass ( $R^2=0.458$ )	Spatial scale
1	0.100			Very broad
2	-0.397	-0.300	-0.251	Very broad
3	-0.511	-0.172	-0.264	Broad
4	-0.024			Broad
5		-0.234	-0.179	Broad
6	-0.067		-0.164	Broad
7	0.071			Broad
8	-0.240	-0.200		Broad
11	-0.223	-0.224		Meso
12	-0.204			Meso
13	0.052			Meso
14	-0.234			Meso
15			-0.185	Meso
19	0.293	0.245	0.344	Meso
22	-0.097			Meso
24	-0.271			Meso
32	-0.368	-0.170		Meso
39		-0.171		Fine
42			0.193	Fine
45	-0.011			Fine
50		0.205	0.202	Fine
53	0.225			Fine
56		-0.179	-0.189	Fine
58		0.164		Fine

In a recent study, Jones et al. (1999) found that the density of fish (number  $m^{-2}$ ) in streams increased with an increase in the development of the riparian forest. Wipfli (1997) suggested that leaves and insects falling from riparian vegetation into the water are trapped in interstices, where they can contribute to enhance habitat quality. According to Miller (1986), riparian vegetation was an important determinant of primary production in a stream. It is a major source of food for stream invertebrates, and it influences the production of aquatic plants by limiting solar energy. Our study suggests that this might also be the case in the littoral zone of lakes.

Patches of high and low forecasted values of relative fish biomass and of *P. flavescens*, *A. nebulosus*, *S. atromaculatus*, and *F. diaphanus* were associated with the fine spatial scale, but no environmental variables could explain the spatial dependency at that scale; in the best cases, the association was weak ( $R^2 \approx 0.05$ ). Spatial structures found at fine scale could be the result of spatial autocorrelation generated by biotic processes, such as reproduction (Legendre 1993). Indeed, species interactions likely occur among individual neighbors at a very fine scale. Several studies have suggested that the decreasing importance of abiotic factors at finer scales could indicate that the biotic factors, such as species interactions, were more important in structuring the communities at finer than at broader scales (Pinel-Alloul et al. 1999). Results at finer scales could also be explained by our sampling strategy. We might not have adequately measured abiotic variability occurring at the finer spatial scales (Weav-

er et al. 1996; Jackson et al. 2001). For instance, some fish might have displayed patterns within the water column by taking up positions at different heights above the substrate (Werner et al. 1977). Unfortunately, our sampling resolution did not segment the water column vertically, so that vertical segregation within the fish community could not be assessed.

**Temporal scale**—The fish community displayed a similar spatial structure in both months. The spatial component explained on average over 36% and 39% of the fish community variability in June and August, respectively. However, compared with June, the environmental variables explained a higher proportion of variance of the fish community descriptors in August. This was particularly apparent for the broader spatial scales for which the difference reached almost 25%. This result could be explained by the more physically structured littoral zones of lakes in late summer than in spring. Macrophyte growth in north temperate lakes reaches its maximum in August; this was also observed in our study in which the density of emergent macrophytes was more than twice as high in August (average  $7.50 \pm 12.70$  stems  $m^{-2}$ ) than it was in June (average  $3.25 \pm 6.38$  stems  $m^{-2}$ ). Several studies have shown the positive relationship between habitat complexity and the abundance of fish (Eadie and Keast 1984; Eklöv 1997; Weaver et al. 1997). Colonization by heterotrophic microorganisms and algae on various substrates (e.g., macrophytes, boulders) also peaks at that period in temperate lakes (Lehmann et al. 1994), thereby providing food resources for fish.

**Species specialization**—The same trends in species assemblages were observed at various spatial and temporal scales in our study. We grouped the species according to the range of spatial scales to which they were associated (Kolasa 1989). Because different features of habitats can be described at different spatial scales, the species of broad ecological range (i.e., generalists) should be more variable at broader spatial scales and use a wider range of spatial scales than species of narrow ecological range (i.e., specialists; Fig. 8). This hypothesis is based on the idea that the generalists are able to easily shift and choose between different types of habitat that provide resource requirements of different qualities.

On the basis of the scale dependency that species displayed, we identified two functional groups in Lake Drouin. The first group, the cyprinids and small-sized species (*N. crysoleucas*, *S. atromaculatus*, and *F. diaphanus*) were associated either with a wide range of spatial scales (from 450 m to 2 km) or at broader spatial scales (broad, very broad), thereby displaying more generalist distributions. They used different types of habitat, including exposed sites, emergent macrophytes, and boulders. According to Morris (1987), species sharing similar habitats should also display similar spatial patterns. This is supported by our results because *N. crysoleucas* and *S. atromaculatus* displayed similar spatial and temporal distributions. They were associated with the same habitat characteristics: a high percentage (75%) of plant cover and the presence of woody debris and rocky substrates. Cyprinids are commonly associated with complex habitat structures, such as dense macrophyte beds and rocky

Table 8. August standardized coefficients (b) of environmental variables that explained significant components of the spatial patterns (PCNM models) of the littoral fish community descriptors at four spatial scales. See Table 2 for the environmental variable codes. Column headings include coefficients of determination ( $R^2$ ) of the models.

	Community composition				Total fish density				Relative fish biomass			
	Very broad ( $R^2=0.720^{***}$ )	Broad ( $R^2=0.140^{***}$ )	Meso ( $R^2=0.130^*$ )	Very broad ( $R^2=0.760^*$ )	Broad ( $R^2=0.289^{**}$ )	Fine ( $R^2=0.047^*$ )	Very broad ( $R^2=0.760^*$ )	Broad ( $R^2=0.331^*$ )	Meso ( $R^2=0.152^{***}$ )			
Riv				0.126*				0.126*				
Lit												
Z				0.109*				0.109*				
S1												
S3												
S4		-0.373*										
S5												
S8												
U1												
U2												
U3												
U4												
U5												
Tree												
Sub	-0.197**		0.209*	-0.194***								
Emer	-0.267***			-0.160**								
Cov	-0.177**		-0.263**									
Fet	-0.749***			-0.802***								
Trib												

\*  $0.01 < p \leq 0.05$ ; \*\*  $0.001 < p \leq 0.01$ ; \*\*\*  $p < 0.001$ .

Table 9. Habitat classification based on the environmental variables associated with the four spatial submodels.

Spatial scale	Theme	Habitat characteristics	Subclass	Description
Very broad (~2,000 m)	Exposed emergent	Wave exposure	High	Fetch: 340–1,406 m
		Emergent macrophyte	Low High	Fetch: 0.00–340 m Emergent (Jun)>8.50 stems m <sup>-2</sup> Emergent (Aug)>42.75 stems m <sup>-2</sup>
Broad (500–1,000 m)	Heterogeneous substrates	Littoral slope	Low	Mean of 0.28
		Substrates	Rocky	Rock and boulder areas
			Woody	Woody debris and tree logs
Meso (300–500 m)	Trees/organic bottom	Riparian use	Trees	Presence of riparian trees
		Organic bottom	High	Percent cover (both months) >75%
Fine (<100 m)	Undescribed	Tributaries	Presence	Very low explained variability (<1%)

substrates (Eklöv 1997; Weaver et al. 1997). They remain forage fish for piscivores during most of their life cycles (Lane et al. 1996), and they have the ability to use different types of habitat in order to exploit peaks of prey abundances and available refuges through the summer. According to Werner et al. (1977), competition among these species is likely to occur within these habitats at a spatial resolution beyond our sampling grain.

The second functional group was composed of species displaying changes in their spatial distributions at different times. These species showed a specialist distribution in June and a generalist distribution in August. *P. flavescens* and *A. nebulosus* displayed a pattern of variability at fine scales in June and shifted to a pattern of variability at the broad scale in August. None of the environmental variables measured could explain their distributions in June, whereas in August, they were associated with rocky substrates. Both species

were found in the same locations of the lake during both months. Several studies conducted on littoral fish species have found that different foraging strategies might preclude competition and favor coexistence between species (Werner and Hall 1976). We are not aware of other studies showing the co-occurrence of *P. flavescens* and *A. nebulosus*; however, our finding in this respect could be explained by temporal segregation in their feeding behavior. The black bullhead is a chemosensory bottom feeder, feeding at night, whereas the yellow perch is an active, diurnal, and wide-ranging hunter (Werner et al. 1977). Therefore, the two species can utilize the same habitat, feeding at different times of the day.

Temporal specialization was also observed for *L. gibbosus*. Variation in this species was associated with the meso scale in June but exhibited a multiscale distribution in August. This species is nesting in early spring. During that period, it is known to use areas of aquatic vegetation (Breder and Rosen 1966) and organic bottom such as that found at the meso scale of our study. In August, *L. gibbosus* displayed a more generalist distribution, being associated with several habitats across the lake (ranging from low fetch/high emergent density to high percentage of plant cover/presence of riparian trees). Our observations agreed with those of Werner et al. (1977), who found that the early August distribution of *L. gibbosus* in Lawrence Lake was evenly spread across habitats, indicating no specific association with environmental characteristics during that period.

Our study suggests that the littoral zone of lakes can be described as a landscape composed of multiple habitat layers of various sizes and qualities influencing the fish community. From a practical perspective, analyses like ours might allow scientists to better plan effective sampling schemes (Sale 1998). For instance, when information suggests that a species, such as *N. crysoleucas*, possesses a multiscale distribution, the use of hierarchical or stratified designs might be preferable to a single-scale approach. From a management perspective, the statistical method applied in our study could help delineate units of conservation for which management actions could be developed, to favor locations with high values of estimated abundance or biomass of certain species. From a fundamental perspective, our study supports the idea that habitat has a hierarchical spatial structure, suggesting the multiscale influences of the environment on the structure of fish communities. The association between fish commu-

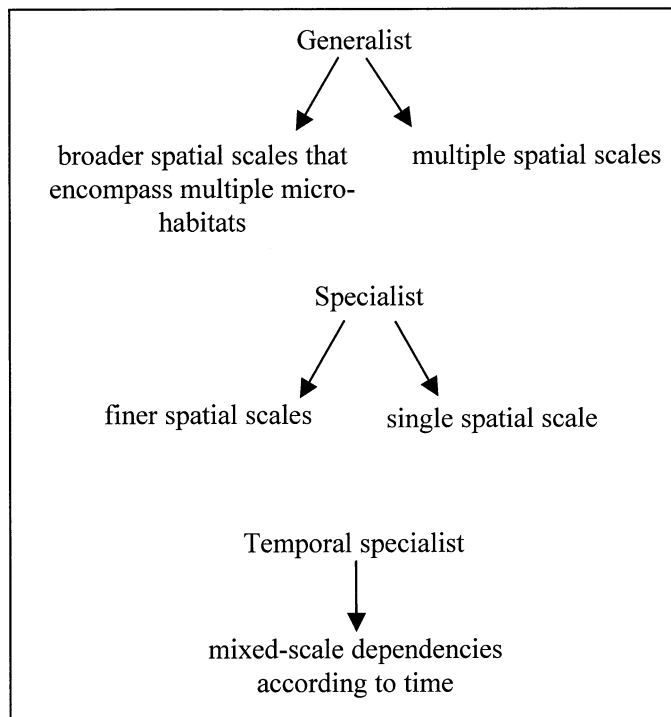


Fig. 8. Schematic structure of three functional groups based on the associations of the species with different ranges of spatial scales.

nity descriptors (community composition, total fish density, and relative fish biomass) and specific environmental variables at different spatial scales supports this point of view. The identification of the relative importance of spatial and temporal variation in the littoral fish community might present a framework for future development of fish habitat models on the basis of the spatial scales at which the fish are responding. It is tempting to speculate that habitat models that are based on variables associated with different spatial scales could improve the predictions of fish-habitat relationships because these models integrate much more information on different habitat requirements of fish species.

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Received: 25 April 2004

Accepted: 20 September 2004

Amended: 13 October 2004