Université de Montréal

Modélisation spatiale multiscalaire de la structure des communautés de poissons lacustres en relation avec les facteurs environnementaux littoraux

par

Anik Brind'Amour

Département des sciences biologiques

Faculté des arts et des sciences

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Université de Montréal
Faculté des études supérieures

Cette thèse intitulée :

Modélisation spatiale multiscalaire de la structure des communautés de poissons lacustres en relation avec les facteurs environnementaux littoraux

Présentée par
Anik Brind'Amour

A été évaluée par un jury composé des personnes suivantes:

André Bouchard
président-rapporteur

Daniel Boisclair
directeur de recherche

Nicolas Lamouroux
examinateur externe

Frédéric Guichard
Examinateur externe

Jacques Bélair
Représentant du doyen de la FES

SOMMAIRE

Les communautés lacustres de poissons littoraux sont exposées à un environnement comprenant une grande hétérogénéité structurale à plusieurs échelles spatiales, variant du millimètre à une centaine de mètres. Par conséquent, les interactions entre les poissons et l'environnement peuvent avoir lieu à différentes échelles spatiales. Des études récentes ont montré que la validité des modèles d'habitats de poissons pouvait être fortement compromise lorsque la structure spatiale de la zone littorale n'était pas intégrée à ces modèles.

L'objectif principal de ma thèse était de modéliser la distribution spatiale multiscalaire des communautés de poissons lacustres en relation avec les facteurs environnementaux. Or, l'étude de l'impact de la structuration spatiale de la zone littorale des lacs sur les communautés de poissons nécessite une technique d'échantillonnage qui soit continue dans l'espace. De nature méthodologique, le Chapitre 1 a servi de base aux trois autres chapitres en montrant la validité du recensement visuel comme méthode d'échantillonnage dans la zone littorale. La seine de rivage, une méthode d'échantillonnage traditionnelle, a été utilisée à titre comparatif. Des descripteurs de la communauté de poissons comparés, la densité totale et la biomasse totale furent visuellement sous-estimées en comparaison avec la seine. Cette divergence entre les deux méthodes fut principalement attribuable à la stratégie d'échantillonnage employée lors du comptage des individus.

La modélisation fut effectuée en deux temps, à l'aide d'une approche multiscalaire, c'est-à-dire en modifiant les attributs relatifs à l'échelle d'analyse spatiale. Dans un premier temps, l'utilisation d'une méthode d'analyse statistique

tenant explicitement compte de la distance entre les unités d'échantillonnage a permis d'observer que les espèces littorales présentaient une variété de patrons de distribution s'échelonnant sur des distances géographiques variant de 100 m à plus de 2 km. Les patrons de distribution associés aux différentes échelles spatiales furent corrélés à différentes variables environnementales, suggérant ainsi la présence de processus écologiques structurant la communauté de poissons spécifique à certaines échelles spatiales (Chapitre 2). Les résultats de ce chapitre ont permis d'émettre certaines hypothèses portant sur la distribution spatiale hiérarchisée des espèces et de leur relation fonctionnelle avec l'environnement. Ces hypothèses furent vérifiées au Chapitre 3, dans lequel nous avons observé si les traits morphologiques et comportementaux des espèces influençaient leur type de patron de distribution spatiale. L'association de certains traits biologiques a permis de regrouper les espèces en trois groupes fonctionnels associés à la position de la bouche et au niveau où elles se nourrissent dans la colonne d'eau (c.-à-d. ségrégation verticale). Les groupes fonctionnels présentaient des différences en ce qui concerne leur association avec différents types d'habitats, suggérant ainsi une ségrégation à la fois verticale et horizontale (entre habitats). L'interprétation de ce chapitre est toutefois mitigée en raison des faibles corrélations obtenues entre les traits et l'environnement.

La diversité des patrons de distribution des espèces sur plusieurs échelles géographiques suggérait notamment l'importance des interactions entre les caractéristiques environnementales et le contexte spatial dans lequel les espèces évoluent. Dans un deuxième temps, cette suggestion fut vérifiée par l'étude de l'impact de la modification du grain de l'échelle d'analyse (c.-à-d. l'utilisation de

différentes tailles d'unités d'analyse) sur la performance des modèles d'habitats (Chapitre 4). Trois tailles d'unités d'analyses, chacune caractérisée par un type de contrainte spatiale, ont ainsi été comparées. La taille de l'unité d'analyse, représentée par le regroupement de sites contigus caractérisés par des variables environnementales similaires (c.-à-d. en tache), a fourni les modèles les plus performants. De plus, l'intégration de variables décrivant l'arrangement spatial des habitats a permis d'observer que les poissons ne sont pas influencés que par les caractéristiques locales, ils sont également influencés par les caractéristiques présentes dans les habitats voisins.

Soulignant la présence de groupes fonctionnels associés à différentes échelles spatiales et l'importance des taches d'habitats dans la structure des communautés de poissons, les résultats de cette thèse suggèrent l'attribution d'une identité et d'une valeur écologique à la variété des habitats, définissant ainsi la zone littorale comme une « diversité fonctionnelle » d'habitats. En regard à la problématique actuelle portant sur la conservation des habitats dans la zone littorale des lacs, les résultats suggèrent que la taille d'un habitat ne saurait représenter le seul critère nécessaire au maintien de cette diversité fonctionnelle. Les interactions entre la taille des taches d'habitat, la distribution spatiale et les caractéristiques environnementales (intrinsèques et extrinsèques) associées à ces taches représenteraient autant de critères à tenir en compte dans l'élaboration des plans de conservation, afin d'assurer le maintien de la diversité des communautés littorales.

<u>Mots clés</u> : communauté lacustre, distribution spatiale, facteurs environnementaux, groupe fonctionnel, habitat, modèles prédictifs, multiscalaire, poissons, zone littorale.

SUMMARY

Fish communities of the littoral zone of lakes are exposed to a structurally complex environment over multiple spatial scales ranging from millimeters to hundreds of meters. Consequently, the interactions between littoral fish communities and their habitat may take place at different spatial scales. Recent papers showed that when ignored, that scale-dependency between fish communities and their habitat could jeopardize the validity of species habitat models.

This thesis had for main objective to model the spatial distribution of littoral fish communities in lakes in relation to environmental factors. The multiscale approach was used in respect to variations in the scale of the spatial analyses. This was done in two steps. At first, we used a statistical approach that took in consideration the distance between the sampling units. Using this approach we observed that the fish community exhibited scale-dependent variability that we grouped in four categories (or submodels), at spatial scales ranging from <100 m to 2 km. These submodels were associated with specific environmental variables, suggesting the presence of scale-dependent ecological processes within the lake (Chapter 2). Results from this chapter allowed us to establish several hypotheses concerning the hierarchical spatial distribution of fish species in relation to their functional relationship with the environment. These hypotheses were verified in chapter 3 in which we tested if species behavioural and morphological traits determined their spatial distribution in lakes. We observed concordance among the species traits suggesting the presence of three functional groups of species according

to the position of the mouth and the location of the fish in the water column (superior-surface, terminal-mid-water, and inferior-benthic). Correlations between the groups of species traist and the environment suggested the presence of habitat segregation along the vertical (water column) and horizontal (habitats) dimensions. However, a constraint interpretation of these results was done because of the low traits-environment correlations observed.

In the second step of the multiscale modelling, we tested the impact of the modification of the size of the analytical unit on the performance of fish habitat models (Chapter 4). Analytical units of three sizes, caracterised by different groupings of the sampling sites, were compared. Models developed with analytical units represented by the grouping of contiguous sampling sites with similar environmental characteristics (i.e. in habitat patch), displayed the highest predictive power. Integration of variables describing the spatial arrangement of habitat within the littoral zone of the lake showed that fish species may not be determined only by the environmental characteristics found within this site but also by conditions found in surrounding locations.

The mulstiscale modeling of the spatial distribution of littoral fish communities in lakes, required a spatially continuous sampling technique. Chapter 1 rooted the other three chapters by validating and establishing the limits in which the visual census technique could be used in this thesis.

Underlying the presence of functional groups associated with multiple spatial scales and the importance of habitat patches in the structure of littoral fish communities, the results from this thesis suggest to assignate an ecological value to

the variety of habitat patches, thereby characterising the littoral zone of a "functional diversity" of habitats. From a conservation point of view, the results also suggest that the size of habitat patches is not the only criteria on which preservation of functional diversity of the littoral zone is based. Interactions between the size of the habitat patch, spatial arrangement of the patches, and the environmental conditions (intrinsic and extrinsic) associated with these patches likely represent significant criteria to maintain the diversity of fish communities in lakes.

Keywords: fish community, littoral zone, lake, multiscale, spatial patterns, habitat, patch, predictive models, functional groups, environmental factors.

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« The scales chosen for analysis are still arbitrary, however : they tend to reflect hierarchies of spatial scales that are based on our own perceptions of nature. Just because these particular scales seem 'right' to us is no assurance that they are appropriate to fish, barnacles, anoles, cattle, or birds.

(Wiens, 1989)

Introduction générale

PROBLÉMATIQUE

L'aménagement grandissant des zones riveraines des lacs entraîne la modification d'éléments riverains et littoraux qui peut avoir des répercussions importantes sur l'habitat du poisson. Au Québec, l'accroissement des aménagements riverains des lacs s'observe depuis une quarantaine d'années. Ces perturbations se concentrent principalement dans les régions les plus peuplées du Québec méridional (Gouvernement du Québec 2004). Parmi les modifications littorales, la substitution d'habitats hautement productifs caractérisés par des structures comportant une grande hétérogénéité structurelle (p. ex. troncs d'arbres morts et bancs de macrophytes), par des habitats de productivité réduite (p. ex. plages de sable) est caractéristique de nombreux lacs aménagés (Christensen et coll. 1996, Radomski et Goeman 2001). Plusieurs travaux ont identifié la perte d'habitats aquatiques comme étant une des causes principales menaçant la conservation des populations et des communautés de poissons des lacs (Evans et coll. 1987, Richter et coll. 1997). En effet, l'altération des habitats littoraux des poissons peut avoir d'importantes conséquences sur la structure des communautés de poissons, puisque ces habitats sont fortement impliqués dans l'organisation des écosystèmes lacustres (Wetzel 1990, Schiemer et Zalewski 1992). De même, de nombreuses espèces s'y retrouvent pour une ou plusieurs parties de leur vie, puisque la zone littorale assure un refuge contre les prédateurs (Mittelbach 1981, Tabor et Wurtsbaugh 1991, Gauthier et coll. 1997), fournit des aires d'alimentation (Werner et coll. 1983, Diehl 1993) et des aires de reproduction (Gafny et coll. 1992).

SÉLECTION D'HABITAT ET NICHES ÉCOLOGIQUES

L'habitat d'un organisme peut se définir comme un espace (physique, chimique et biologique) associé à certaines structures et fonctions nécessaires à l'accomplissement du cycle de vie et au maintien de la population (Hayes et coll. 1996). Dans ce contexte, tous les habitats d'un écosystème aquatique ne sont pas également adéquats pour toutes les espèces à tous les stades de leur vie. La convenance de ces habitats peut varier selon les facteurs environnementaux (abiotiques et biotiques) et les échelles temporelles ou spatiales qui y sont associés (Eckmann 1991, Gaudreau et Boisclair 1998, Fréon et Misund 1999, Gaudreau et Boisclair 2000).

L'importance des facteurs environnementaux dans la sélection d'habitat a été théoriquement développée par le concept de niche écologique. Le terme de niche écologique fut introduit très tôt par Grinnell (1917). Selon cet auteur, la niche d'un organisme représentait tous les sites dont la combinaison de facteurs environnementaux permettait à l'organisme de survivre. Par la suite, Elton (1927) définit la niche comme étant la place qu'un organisme occupe dans un environnement biotique, c'est-à-dire en terme de relation fonctionnelle avec sa nourriture et ses ennemis. En prolongement de la notion de Grinnell, Hutchinson (1958) favorise une approche multidimensionnelle au concept de niche écologique, qu'il considère comme une gamme de variables environnementales (physique, chimique et biotique) pour lesquelles une espèce s'est adaptée. Cette adaptation se traduit notamment par une performance accrue (p. ex. forte abondance) à certains sites. Dans cette définition, chaque variable peut être considérée individuellement comme un gradient au long duquel l'abondance d'une espèce varie (Figure I.1A). Une espèce peut répondre à plusieurs gradients environnementaux qui définissent ainsi sa niche écologique (Figure I.1B). De nos jours, le concept de niche écologique évolue dans un contexte de contrôle multiple où la sélection d'habitat par une espèce est influencée par plusieurs facteurs environnementaux (ou ressources, sensu Magnuson et coll. 1979) pouvant opérer à différentes échelles spatiales et temporelles (Rabeni et Sowa 1996, Jackson et coll. 2001). Par ailleurs, l'étude des patrons spatiaux générés par la sélection d'habitat par les espèces et l'application de ces connaissances dans un contexte prédictif d'élaboration de modèles d'utilisation d'habitat, représente un des principaux buts de l'écologie des communautés (Menge et Olson 1990).

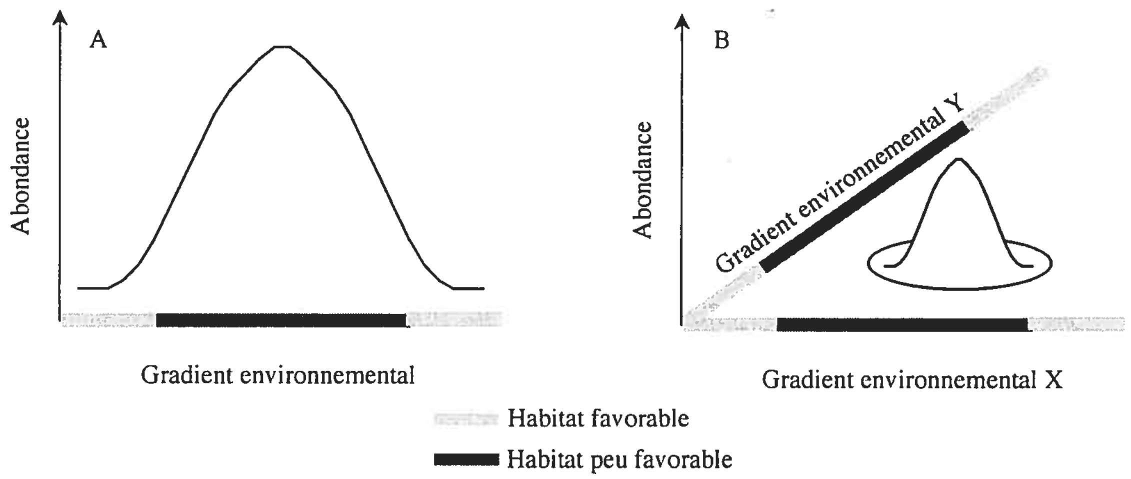


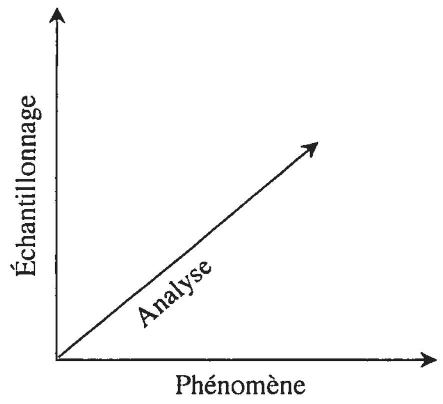
Figure I.1 Schéma représentant la réponse d'une espèce face à (A) un gradient environnemental et (B) deux gradients environnementaux. [adapté de Giller 1984 et Choler 2002].

PATRONS SPATIAUX ET PROCESSUS ÉCOLOGIQUES MULTISCALAIRES

Définis comme étant une configuration ou un arrangement spatial des éléments d'un écosystème, les patrons spatiaux désignent une caractéristique présente dans pratiquement tous les écosystèmes naturels (Taylor et coll. 1978). Les plantes, les animaux et même les variables physiques de l'environnement (p. ex. roches) forment des agrégations pour lesquelles divers patrons de distribution spatiale peuvent être observés (Legendre et Fortin 1989). Ces patrons de distribution spatiale, tant des éléments biotiques que des éléments abiotiques sont contrôlés par divers processus écologiques qui opèrent sur plusieurs échelles spatiales et temporelles. Notre compréhension des processus écologiques générant les patrons de distribution spatiale des espèces repose notamment sur notre capacité d'établir la correspondance entre les échelles de variations biologiques auxquelles se produisent les interactions spécifiques (p. ex. compétition, prédation) et les échelles de variations environnementales qui déterminent les relations entre les espèces et leur environnement (Levin 1999). Or, selon Pascual and Ellner (2000) le couplage de ces échelles de variations est très difficile à obtenir puisque les interactions entre ces dernières varient rarement de façon linéaire. Par exemple, la distribution spatiale d'une espèce peut être influencée par des conditions environnementales (p. ex. degré d'exposition au vent) opérant à des échelles spatiales très larges et présentant un pouvoir prédictif élevé. Cette même espèce peut être aussi influencée par des interactions biologiques (p. ex. prédation) opérant généralement à des échelles spatiales plus fines (Crowder et Cooper 1982) et générant un faible pouvoir prédictif lorsque ces modèles sont basés exclusivement sur des caractéristiques environnmentales.

Notre perception de l'importance relative d'un ensemble de caractéristiques environnementales expliquant la distribution des espèces d'une communauté, varie donc en fonction des échelles spatiale et temporelle auxquelles ces relations sont analysées (Syms 1995). L'étude des patrons spatiaux à l'aide d'une approche multiscalaire, c'est-à-dire à différentes échelles spatiales et temporelles d'analyse, représente un outil essentiel pour comprendre les processus écologiques sous-jacents à la distribution spatiale des espèces et pour déterminer les impacts de ces processus écologiques sur la structure des communautés (p. ex. assemblages d'espèces, structure en taille; Wiens 1976, Menge et Olson 1990).

Dans cette présente thèse, le concept « d'échelle spatiale » est utilisé dans le sens récemment définit par Dungan et coll. (2002). L'échelle spatiale d'une étude repose sur trois dimensions : l'échelle d'échantillonnage (ou d'observation), l'échelle d'analyse statistique et l'échelle des phénomènes écologiques (Figure I.2).



Échelle d'échantillonnage	+	Échelle d'analyse	→	Échelle du phénomène
Taille		Taille		Structure
Forme		Forme		Processus
Distance		Distance		
Étendue		Étendue		

Figure I.2 Représentation graphique du concept d'échelle spatiale définit par ses trois dimensions. [adapté de Dungan et coll. 2002].

Les deux premières échelles sont caractérisées par quatre attributs, soit la taille et la forme de l'unité d'échantillonnage, la distance entre deux unités d'échantillonnage et l'étendue (c.-à-d. longueur, surface ou volume total de l'échantillonnage). Tout changement dans un des attributs modifie l'échelle spatiale et par conséquent l'appréciation des phénomènes écologiques observés.

STRUCTURE DE LA ZONE LITTORALE DES LACS

Dans les lacs, la zone littorale représente l'environnement physique le plus hétérogène, diversifié et productif (Wetzel 1990). Dans la présente étude, elle se définit comme étant la zone qui se retrouve entre l'interface terre-eau s'étendant de la rive, c'est-à-dire juste au-dessus de la zone d'influence des vagues, jusqu'à une profondeur où les eaux chaudes estivales atteignent le fond du lac, c'est-à-dire où il y absence de stratification thermique (Horne et Goldman 1994). Avec sa variété de structures physiques (p. ex. débris de bois, substrats, macrophytes émergentes et submergées) et de ressources alimentaires, la zone littorale se caractérise par une mosaïque de micro-habitats (Boisclair 2001), dont la configuration spatiale et la diversité lui confère une place de choix où se produisent de nombreuses interactions intra et interspécifiques complexes (Werner et coll. 1977). Les communautés de poissons sont donc exposées à un environnement complexe structuré sur plusieurs échelles spatiales variant du millimètre (p. ex. interstices dans les substrats rocheux) à une centaine de mètres (p. ex. distance entre deux tributaires ou entre lits de macrophytes; Weaver et coll. 1997). Par conséquent, les interactions entre les communautés de poissons et l'environnement ont le potentiel d'être fortement spatialisées autant verticalement (dans la colonne d'eau) qu'horizontalement (entre habitats).

Jusqu'à présent, l'étude des patrons de distribution spatiale des poissons littoraux dans les lacs a été fortement polarisée. Elle s'est principalement effectuée à deux échelles spatiales d'observation : à une échelle régionale où le lac est utilisé comme unité d'échantillonnage et à une échelle plus fine où l'unité d'échantillonnage est représentée par quelques types d'habitats prédéfinis (Jackson et coll. 2001). Les échelles utilisées dans ces études sont d'avantage basées sur des choix logistiques (p. ex. engin de pêche, contraintes temporelles et financières) que sur des choix écologiques. Les relations poisson-habitat ainsi développées sont soit basées sur des caractéristiques générales telles, la température moyenne, surface, profondeur maximale (Tonn et Magnuson 1982, Rahel et coll. 1984, Hinch et Collins 1993) ou alors sur des caractéristiques plus précises comme la complexité structurale de certains habitats mesurée à quelques sites dans la zone littorale des lacs (Bryan et Scarnecchia 1992, Rossier et coll. 1996). L'emphase étant mise sur l'importance des processus écologiques à très grande échelle ou l'importance des interactions biologiques aux échelles plus fines. Il y a donc potentiellement des échelles spatiales intermédiaires pour lesquelles divers patrons de distribution spatiale et divers processus écologiques qui demeurent inexplorés.

Depuis près d'une dizaine d'années, la discipline émergente de l'écologie du paysage, s'intéresse à l'influence des patrons spatiaux sur les processus écologiques et plus précisément sur l'impact des patrons en taches (ou patch) sur les communautés écologiques (Wiens et coll. 1993). D'ailleurs, Wiens (2002) a récemment énoncé que « les principes et approches de l'écologie du paysage pouvaient s'étendre et inclure les écosystèmes aquatiques », faisant ainsi référence aux rivières. Alors que la zone littorale des lacs est de plus en plus perçue comme un paysage composé de multiples habitats de tailles et de qualités variables (Chick et McIvor 1994), l'écologie du paysage offre un cadre spatialisé d'étude des relations poisson-habitat dans les lacs.

OBJECTIFS DE RECHERCHE

Cette thèse propose de modéliser la structure spatiale des communautés de poissons lacustres en relation avec les facteurs environnementaux littoraux. La réalisation de cet objectif fut effectuée en utilisant une approche multiscalaire, c'est-à-dire en modifiant certains attributs relatifs à l'échelle d'analyse spatiale. Ces changements ont permis la modélisation de la structure des communautés de poissons à deux niveaux, d'une part dans un contexte decriptif/compréhensif et d'autre part, dans une contexte prédictif/appliqué (Figure I.3).

L'étude de l'impact de la structuration spatiale de la zone littorale des lacs sur les communautés de poissons nécessite une technique d'échantillonnage qui soit continue dans l'espace. Le Chapitre 1 suggère l'utilisation du recensement visuel comme technique d'échantillonnage des communautés de poissons lacustres. Cette technique permet d'effectuer un inventaire des espèces de poissons et des variables environnementales en minimisant les perturbations sur l'habitat (Hall et Werner 1977). L'application de cette méthode dans un environnement lacustre nécessite toutefois certains ajustements. Une analyse comparative des limites avec une méthode d'échantillonnage plus traditionnelle, la seine de rivage, est présentée dans ce premier chapitre.

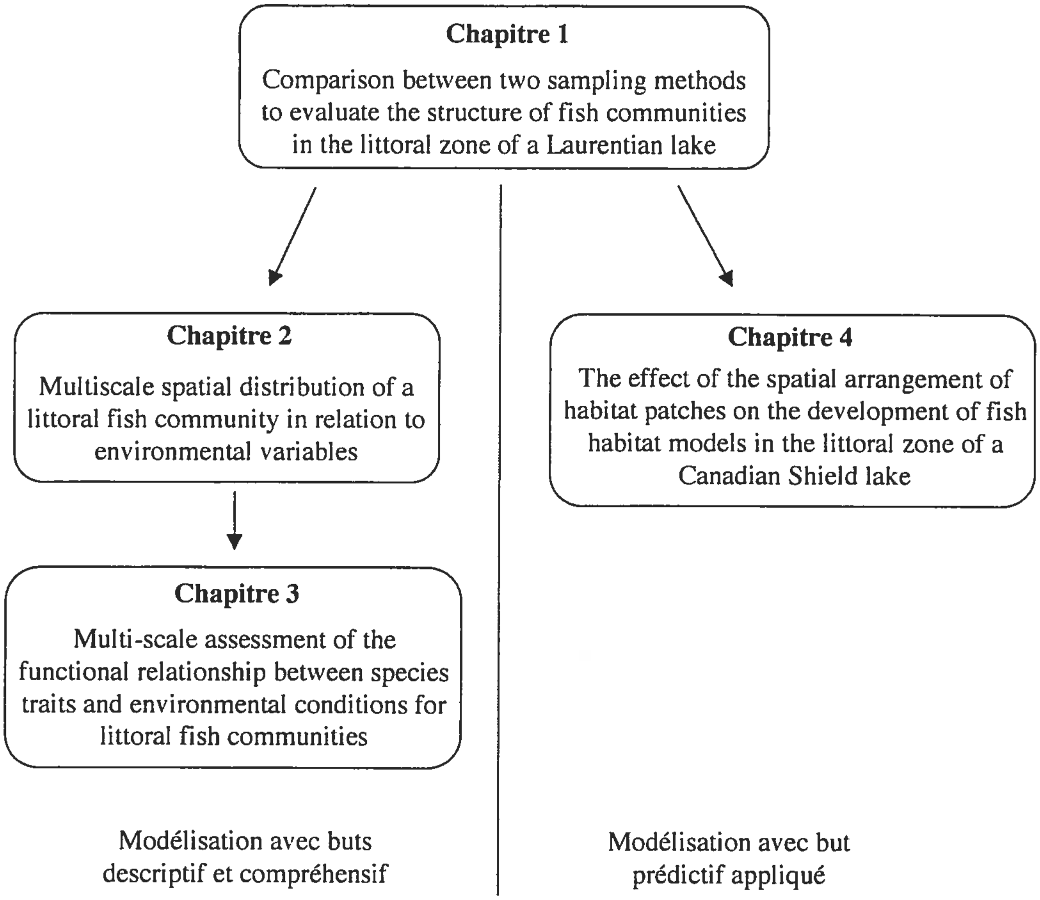


Figure I.3 Schématisation de la structure de la présente thèse en quatre chapitres.

Les approches statistiques offrent un contexte théorique pertinent pour l'étude des patrons de distribution spatiale des espèces littorales et pour l'étude des processus écologiques potentiels générant les assemblages d'espèces dans la zone littorale des lacs. Au Chapitre 2, nous avons appliquée une approche mathématique récemment développée par Borcard et Legendre (2002) et Borcard et coll. (2004) sur une communauté de poissons littoraux d'un lac du Bouclier Canadien (Lac Drouin). Quatre hypothèses furent testées: (1) la variance de la communauté de poissons littoraux d'un lac peut se décomposer en des fractions de variance correspondant à différentes échelles spatiales; (2) la structure de la communauté des poissons perçue à différentes échelles peut être associée à différentes variables environnementales qui fluctuent selon ces échelles; (3) les échelles spatiales et les variables environnementales structurant la communauté de poissons varient sur une échelle temporelle; (4) les espèces se classifient comme généralistes ou spécialistes selon la gamme d'échelles spatiales auxquelles elles sont associées.

La diversité des espèces peuplant la zone littorale des différents lacs et la pluralité de réponses des espèces à l'hétérogénéité spatiale de la zone littorale, soulignent la complexité que peut représenter l'élaboration de modèles d'utilisation d'habitat de poissons littoraux dans les lacs. Alors que les lacs présentent des différences appréciables au niveau de leur composition spécifique, ils partagent généralement les mêmes groupes fonctionnels d'espèces (Díaz et coll. 1998, Nygaard et Ejrnaes 2004). La classification des communautés de poissons en groupes fonctionnels d'espèces partageant des traits biologiques similaires, représente donc un outil facilitant l'élaboration de modèles d'habitat de poissons. Dans le troisième chapitre, nous avons vérifié si les traits comportementaux et morphologiques des espèces de poissons littoraux de deux lacs situés sur le Bouclier Canadien, déterminaient la distribution spatiale de ces espèces. Plus précisément, nous avons vérifié: (1) la présence de groupes fonctionnels résultant de la concordance entre les différents traits comportementaux et morphologiques des espèces, (2) si les espèces constituant un même groupe fonctionnel étaient influencées par les mêmes conditions environnementales et (3) si ces relations traits-environnement possédaient une structure spatiale hiérarchique.

Alors que les chapitres précédents mettaient l'emphase sur des aspects fondamentaux (c.a d. descriptifs et compréhensifs) de la structuration spatiale des communautés de poissons littorales, le Chapitre 4 proposait une application pratique de l'intégration de la structuration spatiale dans des modèles prédictifs d'habitat de poissons. Un nombre grandissant d'études reconnait l'influence non seulement des conditions environnementales locales, mais également de la taille et de l'arrangement spatial des différents habitats sur les communautés de poissons (Essington et Kitchell 1999). Ainsi, le quatrième chapitre testait: (1) l'impact de la taille des unités d'analyse sur la performance des modèles d'habitats et (2) les contributions relativs des variables environnementales locales et des variables environnementales relatives à l'arrangement spatial des sites. Pour ce faire, trois approches furent comparées: (1) une approche dite de sites, dont l'unité d'analyse était équivalente à la dimension des sites d'échantillonnage, (2) une approche dite constante-multiple, dont l'unité d'analyse était constituée de groupements croissants de sites (c.-à-d. 1S, 2S, 3S, etc.) et (3) une approche dite de taches d'habitat, dont l'unité d'analyse correspondait à des groupements de sites contigus partageant les mêmes caractéristiques environnementales. En comparant ces diverses approches statistiques, le quatrième chapitre se voulait une contribution à une meilleure utilisation des modèles prédictifs d'habitat à l'échelle d'un lac.

Chapitre 1

Comparison between two sampling methods to evaluate the structure of fish communities in the littoral zone of a Laurentian lake

A. Brind'Amour and D. Boisclair

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ABSTRACT

The results of beach seining were compared with visual surveys, in habitats showing a gradient of macrophyte densities in Lake Drouin, Québec, Canada. Six community descriptors (species density, total fish density, relative abundance per species, presence or absence of given species, size structure of the fish community and total biomass of the fish community) were used to compare the sampling methods. Most of the fish community descriptors obtained by visual surveys were estimated with an accuracy similar to that of beach seining. Both methods sampled the same number of species (eight out of nine). Visual surveys assessed the relative abundance of the yellow perch *Perca flavescens* and white sucker *Catostomus commersoni* with an higher accuracy than the beach seine. The greatest discrepancies between the two sampling methods were for total fish density and the total fish biomass. Because of the sampling strategy, both descriptors were underestimated by visual surveys, notably in the higher macrophyte density. In a broad community survey to determine the relative importance of species abundance, the visual survey was effective and could be used to develop a within-lake regular and fine-scale sampling design of the spatial arrangement of fish communities and their habitats.

INTRODUCTION

The purpose of fish habitat models is to describe and eventually to predict the effects of natural and anthropogenic perturbations on measures of fish performance (e.g. abundance, survival, reproduction, growth). Many studies developed relationships between measures of fish performance and environmental conditions (Werner et al. 1977, Brazner and Magnuson 1994, Randall et al. 1996). The identification of the proper spatial scale (s) at which the existence of such relationships should be tested and the relative significance of processes occurring at these scales, however, remains the key problem of habitat models (Lewis et al. 1996, Mason and Brandt 1996). Fundamental contributions to the development of spatially-explicit (Brandt et al. 1992) and individual-based models (Kocik and Ferreri 1998, Essington and Kitchell 1999) illustrate the recognition that fish may not only be affected by local environmental conditions, or by the quantity of habitats possessing specific key characteristics, but also by the spatial arrangement of habitats (Essington and Kitchell 1999). Proper analysis of the effect of the spatial arrangement of environmental conditions on fish requires a spatially continuous sampling design. The feasibility of conducting spatially continuous sampling surveys depends on fish community complexity, habitat structure, and methodological limitations.

The littoral zone of lakes is generally recognised as a productive, diverse, and physically heterogeneous environment (Wetzel 1990). As such, it bears a particularly interesting status for studies on biodiversity, conservation, and management. Beach seining is one of the most common methods used to sample the fish community of the littoral zone, because it allows the investigator to identify, count, and collect a suite of variables about the fish captured (Pierce et al. 1990). Furthermore, the volume or the surface area sampled by seining may be estimated with a precision that surpasses that of many other methods (gill nets, trap nets, etc). Because of logistical limitations, it is difficult to conceive that seining could be used to provide a spatially continuous description of fish communities in the littoral zone of lakes. Visual sampling, like seining, is subjected to the potential problems of fish avoidance and cryptic behaviour (Harmelin-Vivien et al. 1985). Benthic-oriented or small size species may hide within coarse substrate interstices or can escape beneath the lead line when seine approaches (Parsley *et al.,* 1989). Visual sampling may allow the investigator to count and identify fish, and to estimate the area sampled. These are prerequisites for the development of a regular and fine-scale sampling design of the spatial arrangement of fish communities and of their habitats.

No method can be expected to provide a complete and flawless quantitative description of the structure of the fish community in the littoral zone of lakes (Weaver et al. 1993). The comparison of different methods, however, may allow an increase in the understanding of the information provided by the analysis of data based on a specific sampling approach. The objective of the present study was to compare the descriptors (species density, total fish density, relative abundance per species, presence or absence of given species, size structure of the fish community and total biomass of the fish community) of the structure of the littoral zone fish community obtained by seining with values obtained by visual surveys. This comparison was performed to identify those variables obtained by visual surveys that may be estimated with an accuracy equal to, or higher than, that of seining and, consequently, assessing the variables that may be the subject of spatially continuous sampling.

MATERIALS AND METHODS

Study lake

Sampling was conducted in Lake Drouin (Lanaudière Region of Québec, Canada; 46°09' N : 73°55' W) during the spring and summer periods of 2001 (Figure 1.1). Lake Drouin was selected for this study because it has a diversified littoral zone with woody debris, rocky substrate, sand beaches, and patches of macrophytes of mixed species such as water shield *Brassenia schreberi*, pipewort *Eriocaulon aquaticum*, Eurasian milfoil *Myriophyllum spicatum*, and waterlillies *Nymphea sp.* This mesotrophic lake has a surface area of 31 ha and a maximum depth of 22 m. 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 ranges from 4°C to 8°C. The thermocline forms at 4.5 m depth in mid-June and breaks down in early October.

Sampling procedures

The structure of the littoral zone fish community was assessed at 10 sites in Lake Drouin. The number of sites surveyed corresponded to the maximum number of seine hauls (*c.* 40 min per seine haul including collecting fish data) that could be completed within a sampling interval of *c.* 6 h (from 900 hours to 1500 hours). This criterion was used in an attempt to minimise the effect of potential changes on fish community attributes over the diel cycle (dusk, mid-day, dawn, night; Keast and Harker 1977).

The 10 sites were selected on the basis of information collected during a pre-sampling survey (6 June 2001). During this pre-sampling phase, the littoral zone at any potential sampling site was described using average water depth, substrate composition, and potential for macrophyte development (Table 1.1). Average water depth in each sampling site was measured at three locations along a transect perpendicular to shore (25, 50 and 100% of the width of a sampling site). The average of the three measures was used in the statistical analysis. Sites with a silty substrate on which dead macrophytes could be seen were considered as potential sites for macrophyte growth.

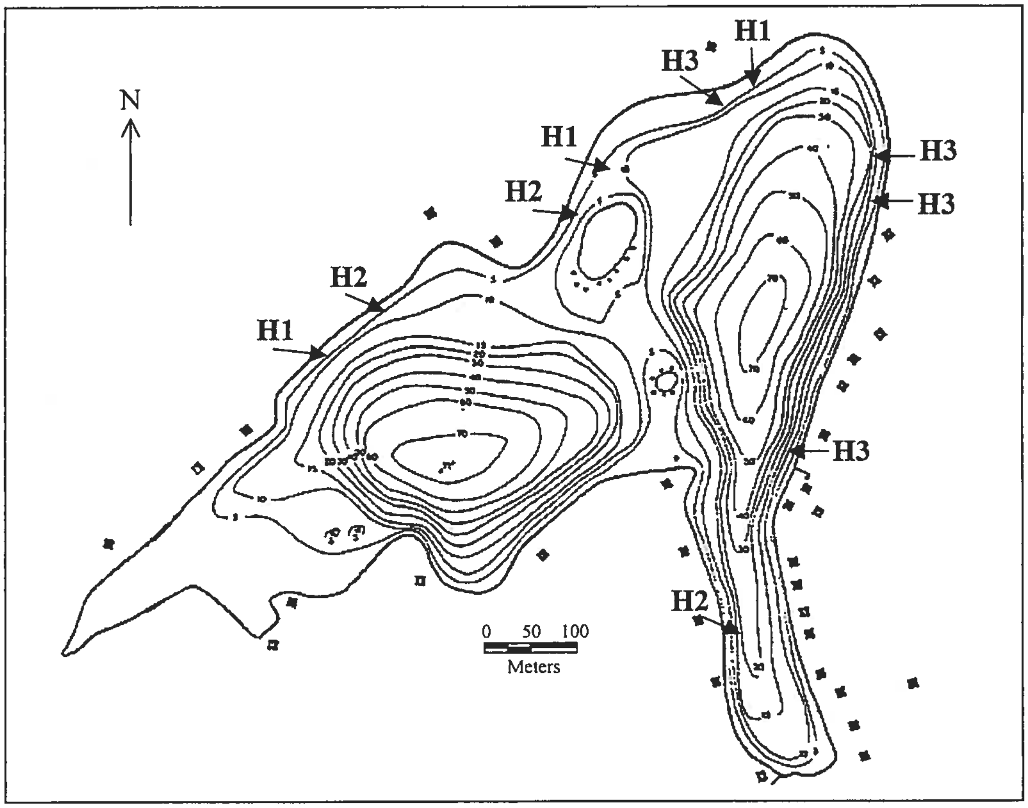

Figure 1.1 Location of the ten sites classified by the three classes of habitat (H) at Lake Drouin (Quebec). Black squares along the lake contour represent houses and cottages.

Table 1.1 Description of the four environmental characteristics. Macrophyte density was estimated by the individual per m^2 and the different types of substrate were expressed as binary variables.

Site	Macrophyte density (stem m^{-2})[1]	Macrophyte density (stem m^{-2})[2]	Average water depth (m)	Sand	Boulder	Woody debris	Habitat category
1	3.50	0.50	2.34	1	0	0	2
2	7.25	12.25	0.84	0	1	0	3
3	0.00	0.00	1.35	1	0	0	1
4	32.75	42.75	0.89	0	1	0	3
5	0.25	0.75	3.01	1	0	0	1
6	1.80	1.00	2.19	1	0	0	2
7	0.50	0.00	2.52	0	1	0	1
8	2.25	13.75	2.58	0	0	1	2
9	32.25	14.75	2.52	1	0	0	3
10	1.50	7.75	1.81	0	0	1	2

[1] = June, [2] = August.

The sampling sites used were selected using three criteria: the surface area of the sites, the within-site homogeneity, and the among-site diversity. The minimum surface area of the sampling sites (200 m^2) was determined by the maximum surface area sampled by our seine and by our intention to associate site-specific series of fish community descriptors to well-defined habitat types. The length of a sampling site (35 to 70 m) was defined by its dimension along shore. The width of a sampling site (5 to 10 m) was determined by the distance from shore to the 3 m depth isobath. The limit of 3 m was adopted because it corresponded to the depth at which all fishes observed could be identified and counted in the lake. Sampling sites had to possess relatively homogenous attributes in respect to a given combination of variables used to describe the sampling sites over at least 80% of their surface area (160 m^2). Finally, the sampling sites selected had to cover the complete range of combinations of average water depth, substrate composition, and potential macrophyte density in the littoral zone of the lake.

The sampling phase consisted in the estimation of water transparency, macrophyte density, and fish community structure at the ten sampling sites selected during the pre-sampling phase. Water transparency at each sampling site was measured with a Secchi disk above the 4.5 m depth contour at *c*. 1400 hours every day that the visual surveys were done. Water transparency was always equal to 4.5 m (bottom). Thus water transparency probably did not limit the capacity to perform visual surveys from shore to the 3 m depth. Among-site variations of water transparency were minimal and they had no effect on the comparisons of fish community data among sites.

Sampling for macrophyte and fish were both performed from 19 to 26 June (further referred to as June) and from 28 July to 5 August 2001 (further referred to as August). This strategy was adopted to insure adequate temporal matching between data collected for macrophytes and fish. The density of macrophytes at the ten sites was estimated by two snorkellers on 25 June and 2 August 2001. Whenever fish sampling was conducted on the same day as macrophyte sampling, the fish sampling was always done prior to the sampling of macrophyte to avoid fish disturbance. The density of macrophytes at each site was estimated in four randomly selected 1 m^2 quadrats (a 1 m^2 frame was thrown from centre of the sampling site in different directions within each site). The number of stems from submersed, from emergent, and from leaf-floating forms per 1 m^2 was counted and summed. The average number of stems from the four replicates was used in the statistical analysis.

The sampling of the fish community using the seine and the visual surveys was conducted between 19 and 26 June 2001 and between 28 July and 5 August 2001. A number (from 1 to 10) was assigned to each sampling site and represented the temporal order in which they were sampled during one day. This order was maintained for the different sampling days and sampling methods (seine and visual samplings).

Seining was performed on 19 and 23 June and on 28 July and 5 August. Seining was done during the day between 1000 and 1600 hours with a 50 m x 3 m beach seine (mesh size = 1 cm). At each sampling site, one seine haul of rectangular shape that covered a surface area of 260 m^2 (S.D. = 51.639) was performed from a small boat propelled by an electric motor to minimise noise and fish disturbance. The seine was deployed such that it always extended to the 3 m depth isobath. The fishes captured were immediately identified, counted, and measured. The total length (L_T, to the nearest 0.25 cm) of a maximum of twenty fish per species was measured. The twenty fish per species were selected to cover the complete size range sampled for this species. The ratios between the number of fish measured over the number of fish captured were over 75% for all the species, except for *Lepomis gibbosus* (Linnaeus) for which 38% of the individuals captured were actually measured. While seining, a snorkeller was prepared to free the seine from obstacles whenever necessary. This strategy was used to improve capture efficiency.

Visual surveys used to describe the fish community were conducted on 25 and 26 June and on 3 and 4 August during the day between 1000 and 1400 hours using a modified version of the technique described by Harmelin-Vivien et al. (1985). This technique requires two observers who snorkel at the water surface performing zigzags over the complete length and width of a sampling site following a trajectory that was globally parallel to shore. During such sampling, the distance between the two observers was *c.* 4 m. This technique allowed the observers to cover 90% of the total area of each sampling site. The observers maintained a constant swimming speed of *c.* 10 m min^{-1} to minimise fish disturbance (Eklöv 1997). Data were noted on polyvinyl chloride (PVC) cylinders that snorkellers wore around their forearm. Snorkellers identified the species, the relative abundance, and the approximate size of the fish observed as they progressed along their respective transect. The relative abundance of fish was defined in six classes: class 1 = 1 individual; class 2 = 2 individuals; class 3 = 3 individuals; class 4 = 4-5 individuals; class 5 = 6-9 individuals and class 6 = 10 individuals and more. Each fish was also categorised according to its size (Table 1.2). The classification of fish size was based on specific ecological information extracted from Scott and Crossman (1973). For instance, the distinction between small individuals (juveniles) and large individuals (adults) for *Catostomus commersoni* (Lacepede), was based on the minimum size (160 mm) at which the individuals shift from plankton feeding to bottom feeding. This approach, applied to all fish species present in Lake Drouin resulted in the definition of three size classes: SC_1 = shorter than 110 mm L_T; SC_2 = 110-160 mm L_T; SC_3= longer than 160 mm L_T.

Computations

The fish community was characterised using six descriptors: total number of species, total fish abundance, relative abundance per species, presence or absence of given species, size structure of the fish community, and total biomass of the fish community. Each of these descriptors was estimated for each sampling site using data collected by seining and by visual surveys. Since the surface area sampled varied among the sampling sites, the total number of species and the total fish abundance were calculated per unit area. This operation led to the creation of two additional descriptors of the fish community: the species density and total fish density. These newly estimated descriptors were used in the statistical analyses instead of the original abundance descriptors. The relative abundance per species was calculated by converting species abundances from each site into a percentage. The size structure of the fish community at each sampling site was described by the percentage of fish (C_i) in the three size classes (SC_1; SC_2; SC_3):

$$C_i = (n_i N^{-1})\ 100 \qquad (1)$$

where n_i is the number of fishes of a given size class i and N is the total abundance of fish at a sampling site. Since the abundance data (n_i) obtained with the visual surveys were collected in classes, we transformed them to abundance values as follow: 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 discontinuous to continuous allowed us to compute the community descriptors.

Table 1.2 Size range, measured with a precision equal to ± 2.5 mm, for each species sampled in the community. The asterisk identifies the species sampled with the seine and the visual surveys. Common names are in parenthesis.

		L_T range	Method	
Species	Code	(mm)	Seine	Visual
Pimephales promelas Rafinesque (fathead minnow)	Pipr	40-90		*
Perca flavescens Mitchill (yellow perch)	Pefl	55-230	*	*
Lepomis gibbosus Linnaeus (pumpkinseed)	Legi	30-195	*	*
Ameriurus nebulosus Lesueur (brown bullhead)	Amne	50-190	*	*
Notemigonus crysoleucas Mitchill (golden shiner)	Nocr	65-225	*	*
Semotilus atromaculatus Mitchill (creek chub)	Seat	55-135	*	*
Catostomus commersoni Lacepede (white sucker)	Caco	55-320	*	*
Fundulus diaphanus Lesueur (banded killifish)	Fudi	50-85	*	*
Umbra limi Kirtland (central mudminnow)	Umli	50-100	*	

The total biomass (B_T) of fishes for any combination of species and size class was estimated as:

$$B_T = \Sigma\, n_{i,s}\, M_{i,s} \qquad (2)$$

where $n_{i,s}$ is the number of fish per species per size class and $M_{i,s}$ is the average fish mass (grams) per species per size class estimated using the length-mass relationships in Schneider et al. (2000) and from relationships estimated in our laboratory for

Laurentian lakes (Comeau & Boisclair, unpublished). The total fish biomass was also divided by the surface area of each sampling site.

Statistical analyses

The 10 sites were partitioned among three groups of habitat defined by average water depth, composition of the substratum and density of macrophytes. A discriminant analysis using a stepwise method was used to estimate the linear combinations of the environmental variables (average water depth, substratum composition and macrophyte density) that were maximally effective in distinguishing the groups of habitats. Because the discriminant analysis suggested that only macrophyte density significantly contributed to the variation among sampling sites, the different habitat types (H) were defined according to macrophyte densities: H1, low macrophyte density ranging from 0.00 to 1.80 stems m^{-2}; H2, medium macrophyte density ranging from 0.50 to 13.75 stems m^{-2}; H3, high macrophyte density ranging from 7.25 to 42.75 stems m^{-2}. The new habitat variable was subsequently used as a main factor in the statistical analysis comparing the two sampling methods. This discriminant analysis was carried out with SPSS (SPSS, 1999).

Statistical analyses on the multivariate fish community descriptors were done using a multivariate analysis of variance (MANOVA) design with covariates. Statistical analyses on the univariate fish community descriptors were done using an analysis of variance (ANOVA) design with covariates. The main factors in the MANOVA and the ANOVA were the sampling method (M), the type of habitat (H), and the sampling month (Mo). Because the fish sampling using the seine and the visual surveys were not conducted on the same day, two dummy variables representing the sampling days were used as covariates. These dummy variables were orthogonal with each other (*i.e.* their sum = 0). The first dummy variable coded for the seine sampling days: with 1 for the first day of the seine sampling, with –1 for the second day of seine sampling, and with 0 for the 2 days of visual surveys. The second dummy variable was coded with 0 for the 2 days of seine sampling and 1 and –1 for the 2 days of sampling with the visual surveys. The site numbers defining the temporal order in which the sampling was conducted were also used as covariates. A significant effect of the factor M or the interaction terms M x H, M x Mo or M x H x Mo was interpreted as a difference between the two sampling methods in describing the fish community. Since the main interest was the comparison between the sampling methods, only the results for those terms were discussed. Statistical analyses were carried out with SPSS (SPSS, 1999), using a significance threshold of 0.05. A posteriori multiple comparisons were done on the 95% confidence intervals of the interaction terms (M x H, M x Mo, M x H x Mo) using the Bonferroni correction for multiple testing (Sokal and Rohlf 1995). Partial correlation analyses, controlling for the site numbers, were conducted on fish community descriptors showing discrepancies between the two sampling methods. Normality was tested using the Shapiro-Wilks statistics (Zar 1984). Heterogeneity of variance was sometimes observed, but the analysis of variance is relatively robust to unequal variances provided that a fixed model is used (Bray and Maxwell 1985). The Hellinger transformation (Legendre and Gallagher 2001) was computed on the presence or absence of species, and size structure, while base $\log_{10}$ transformation was performed on species density, total fish density, and total biomass data.

RESULTS

Classification results showed that 70% of the original groups and 60% of the cross-validated groups were correctly classified using the three types of habitat at each sampling sites. Results of the discriminant analysis also suggested that only macrophyte density significantly contributed to the variation among sites (June: ANOVA, df = 1 and 7, $P < 0.05$; August: ANOVA, df = 1 and 7, $P = 0.049$). Hence, the effect of the factor habitat (H) in the statistical analysis was interpreted as an effect of macrophyte density. The macrophytes were grouped in three categories of densities. Low macrophyte density, ranged from 0.00 to 1.80 stems m^{-2}; medium macrophyte density, ranged from 0.50 to 13.75 stems m^{-2}; high macrophyte density, ranged from 7.25 to 42.75 stems m^{-2}. Since the density of macrophytes did not vary significantly among months (ANOVA, df = 1 and 18, $P = 0.400$), the grouping of the sites was the same for both months (Table 1.1).

Habitat classification

The sampling sites varied in average water depth, substrate composition, and average macrophyte density (Table 1.1). Average water depth ranged from 0.84 m to 3.01 m among sites. Most of our sampling sites (70%) had an average water depth greater than 1.5 m while 20% had an average smaller than 1 m. The bottom of 50% of the sites comprised sand as a dominant substrate while 30% and 20% of the sites were mostly composed of boulders and woody debris respectively. The density of macrophytes ranged from 0.00 stems m^{-2} to 42.75 stems m^{-2} with an average of 8.78

stems m^{-2}. The macrophytes varied significantly among the sampling sites (ANOVA, df = 9 and 10, $P < 0.01$).

Community descriptors

Species density —Nine fish species were sampled (Table II). The beach seine captured eight species but never captured *Pimephales promelas* (Rafinesque) while the visual surveys also sampled eight species but never sampled *Umbra limi* (Kirtland). Hence, the sampling methods shared seven of the nine species collected. The number of species captured using the seine in single sampling sites ranged from 0.003 species m^{-2} to 0.035 species m^{-2} while the number of species observed during visual surveys ranged from 0.003 species m^{-2} to 0.025 species m^{-2}. On average, the seine (mean number of species per m^2 = 0.018) captured 25% more species than observed during the visual surveys (mean number of species per m^2 = 0.014), but the difference between sampling methods (M) was not significant (ANOVA, df = 1 and 65, $P = 0.074$). The interaction terms M x H (ANOVA, df = 2 and 65, $P = 0.823$) and M x Mo (ANOVA, df = 1 and 65, $P = 0.349$) were not significant. This was taken as an indication that species density varied similarly among the three densities of macrophyte and between the two months for both sampling methods.

Total fish density —An overall total of 3207 fishes were observed using the two methods during the two sampling months. Total fish density within sampling sites ranged from 0.006 to 0.950 fish m^{-2} (mean ± S.D.; 0.252 ± 0.229 fish m^{-2}) for the seine and ranged from 0.010 to 0.170 fish m^{-2} (0.081 ± 0.038 fish m^{-2}) for the visual surveys. Total fish density estimated by seining (low, 0.149 ± 0.185 fish m^{-2}; medium, 0.276 ± 0.186 fish m^{-2}; high macrophyte density, 0.364 ± 0.275 fish m^{-2}) was generally higher than values obtained during visual surveys (low, 0.069 ± 0.029 fish m^{-2}; medium, 0.079 ± 0.039 fish m^{-2}; high macrophyte density, 0.102 ± 0.039 fish m^{-2}). Total fish density increased by 40% (for the beach seine) and 20% (for the visual surveys) as macrophyte density increased. The total fish density estimated with the seine was 0.1% (low macrophyte density) to 56% (high macrophyte density) higher than values obtained by visual surveys. As indicated by the significant interaction term M x H (ANOVA, df = 2 and 65, $P = 0.027$), the increase in total fish density with the increase of macrophyte density was more important for the seine than for the visual sampling. Both sampling methods indicated higher fish density in June (beach seine, 0.342 ± 0.216 fish m^{-2}; visual surveys, 0.087 ± 0.039 fish m^{-2}) than in August (beach seine, 0.185 ± 0.219 fish m^{-2}; visual surveys, 0.079 ± 0.036 fish m^{-2}). Total fish density estimated in June with the seine was 64% higher than values obtained using visual surveys. However, this difference decreased to 11% in August. Accordingly, the interaction term M x Mo was significant (ANOVA, df = 1 and 65, $P = 0.007$). This confirmed that the decrease in total fish density from June to August was more important for the values obtained using the seine than estimates based on visual surveys. A partial correlation analysis was done on the total fish density to see the relation between the two sampling methods (Pearson $r = 0.55$, $n = 40$, $P < 0.001$).

Relative abundance per species —The average percent contribution of any given species to the fish community ranged from 1.5% to 72% using the seine and from 3% to 56% using the visual surveys. Both sampling methods indicated that *L. gibbosus* was, on average, the most abundant species (mean ± S.D.; seine, 72.2 ± 17.9%; visual surveys, 56.0 ± 25.1%). *Semotilus atromaculatus* (Mitchill) (seine, 9.0 ± 11.7%;

visual surveys, 13.1 ± 15.6%) and *Notemegonus crysoleucas* (Mitchill) (seine, 6.8 ± 9.9%; visual surveys, 10.7 ± 13.2%) were the following two most abundant species for both sampling methods. Taken together, these three species represented more than 88% of the fish community sampled by the seine and more than 79% of the fish community observed during the visual surveys. Relative abundance of the remaining four species of the fish community, *Perca flavescens* (Mitchill), *C. commersoni*, *Ameriurus nebulosus* (Lesueur), and *Fundulus diaphanus* (Lesueur) was 1.5, 0.5, 3.9, and 6.1% respectively for the seine and 4.9, 2.7, 2.9, and 9.7% respectively for the visual surveys. Of the seven species analysed, *L. gibbosus*, *P. flavescens*, and *C. commersoni* varied significantly among sampling methods (M; MANOVA, df = 6 and 60, *P* = 0.003). Abundance estimates of *L. gibbosus* obtained using the seine were, on average, 25% higher than corresponding values resulting from visual surveys. In contrast, the average number of *P. flavescens* and *C. commersoni* observed during visual surveys was respectively 107 and 134 % higher than abundance estimates obtained during seining. The interaction terms M x H (MANOVA, df = 12 and 122, *P* = 0.098) and M x Mo (MANOVA, df = 6 and 60, *P* = 0.301) were not significant. Hence, both sampling methods showed similar efficiency in sampling the fish community among the three densities of macrophyte and between both sampling months.

*Presence or absence of species —L. gibbosu*s was the most common species with a frequency of occurrence of 100 % with both sampling methods. In contrast *C. commersoni* was observed only in two sites (frequency of occurrence of 18%) with the seine and in four sites (frequency of occurrence of 23%) with the visual sampling.

The frequency of occurrence for the other species ranged from 38 to 80% irrespective of the methods. The presence-absence data were not significantly affected by the methods but the statistics approached the significance threshold (MANOVA, df = 7, and 59, $P = 0.052$). The interaction terms M x H (MANOVA, df =14 and 120, $P = 0.298$) and M x Mo (MANOVA, df =7 and 59, $P = 0.242$) were not significant. This suggests that both sampling methods similarly estimated the presence-absence of the fish species among the three macrophyte densities and among the two sampling months.

Size structure —Small fishes (SC_1) represented on average 93% of the fishes (range = 68 to 100%) in the seine estimates in comparison to an average of 86% (range = 49 to 100%) in visual surveys. Medium fishes (SC_2) represented on average 7% of the fishes captured (range = 0 to 32%) using the seine, whereas it represented an average of 13% of the fishes estimated (range = 0 to 52%) using visual surveys. Large fishes (SC_3) represented less than 1% (range = 0 to 3%) in the seine estimates and nearly 1% (range = 0 to 18%) in visual surveys. Among the three size classes, only the SC_1 displayed a significant difference between the sampling methods (M; MANOVA, df = 3 and 63, $P < 0.001$). The interaction term M x H was significant (MANOVA, df = 2 and 65, $P = 0.014$). This suggests that the proportion of SC_1 estimated using both methods varied differently among habitats. The proportion of the SC_1 estimated in the habitat with the higher density of macrophyte was 10% higher using the seine (mean = 96.3%) than estimated using the visual surveys (mean = 86.9%). In the habitat with the medium density of macrophyte, the average percent contribution of SC_1 estimated with the seine (average = 94.2%) was only 4% higher than the value obtained using the visual surveys (average = 90.6%). The interaction term M x Mo indicated that both methods sampled the same proportions of SC_1, SC_2, and SC_3 in June and August (MANOVA, df 3 and 63, $P = 0.317$).

Total fish biomass —The estimator total biomass of the fish community ranged from 0.03 to 11.14 g m^{-2} using the seine and ranged from 0.12 to 3.23 g m^{-2} using visual surveys. The beach seine value (mean ± S.D.; 2.64 ± 2.44 g m^{-2}) displayed on average twice the biomass per m^2 than the visual surveys (1.14 ± 0.92 g m^{-2}) (ANOVA, df = 1 and 65, $P \leq 0.001$). The interaction terms M x H (ANOVA, df = 2 and 65, $P = 0.181$) and M x Mo (ANOVA, df = 1 and 65, $P = 0.225$) were not significant. These interactions indicate that both sampling methods similarly estimated the total biomass of the fish community across the three macrophyte densities and across the two sampling months. A partial correlation analysis was done on the total fish biomass to see the relation between the two sampling methods ($r = 0.57$, $n = 40$, $P < 0.001$).

DISCUSSION

The present study compared descriptors of a littoral fish community obtained by seining to those acquired by visual surveys. This comparison was performed with the aim of identifying the variables that may be estimated by visual sampling with an accuracy at least equal to that of seining. Our results showed that the two sampling methods often provided similar results in the assessment of most of the descriptors of the littoral fish community.

The total number of species, a global community metric used to describe the general structure of the fish community, did not differ between the sampling methods. Both methods detected eight of the nine species found in the littoral zone of the lake studied. The list of species obtained by the two methods, however, shared seven of the eight species recorded per method. The two sampling approaches showed that as the density of macrophytes increased, the total number of fish species also increased. The capacity of heterogeneous habitats, such as weed beds, to provide a refuge to fishes, and hence, to allow the occurrence of a higher number of fish species than other habitats, has been observed in many studies (Rahel 1990). In a recent study comparing visual surveys to experimental gillnets, Pratt and Fox (2001) also found a positive relationship between the number of species and the importance of the cover provided by macrophytes. The present study indicates that seining and visual surveys detected more fish species in habitats having medium and high macrophyte density than in habitats characterised by low macrophyte density. Hence, the study suggested that both sampling methods allow the observation of a similar number of fish species within the range of habitat structure present in the study lake.

Comparison of species composition using the presence-absence and the relative abundance data indicated the dominance of a few abundant species. This characteristic of fish communities has been observed in temperate rivers and lakes (Lohr and Fausch 1997, Pratt and Fox 2001). The centrarchids and cyprinids were the two most abundant families observed by both methods, with *L. gibbosus, N. crysoleucas* and *S. atromaculatus* representing >88% of the fish community in the seine and >79% of the fish community in the visual surveys. The ability of the seine and the visual surveys to evaluate the community composition was similar using the presence-absence data. However, visual surveys were more accurate than seining to evaluate community composition based on the relative abundance of certain species.

For instance, species such as *C. commersoni* and *P. flavescens* were greatly underestimated (107 and 134 %, respectively) with the seine in comparison to visual surveys. Low efficiency of the seine for benthic species inhabiting lower parts of the littoral zone, has been observed by several authors (Lyons 1986, Parsley et al. 1989, Pierce et al. 1990). For instance, Parsley et al. (1989) evaluated the capture efficiency of different species using the seine. They suggested that the efficiency of the seine was related to the typical position of fish species within the water column. Benthic-oriented species may be able to escape beneath the lead line of the seine and hence decrease the efficiency of the seine for these species. In a study comparing relative abundances of fish families using the seine and the visual surveys in three Connecticut rivers, Goldstein (1978) found that the relative abundance of *C. commersoni* was 100% greater with the visual surveys than with the seine. Although his study was conducted in rivers, his results are in agreement with the present study. However, this study took into account different types of habitat, which permitted a determination of the ability of each method to sample individual species in relation to different macrophyte coverage.

The size structure of the fish community of Lake Drouin based on data obtained using the seine was similar to that obtained during visual surveys. Nearly 90% of the fishes collected by seining or observed during visual surveys were <110 mm. Both methods showed that fishes >110 mm (medium and large sizes) preferred the habitats displaying high density of macrophytes. However, the seine captured 4 and 10% more fishes from the first size class (<110 mm) in the medium and high density of macrophyte than estimated by visual surveys. Although 4 and 10%

represent small differences, the high selectivity of the seine towards smaller fish species has been observed by other studies (Hayes 1989, Parsley et al. 1989, Weaver et al. 1993).

The major discrepancy between the two sampling methods was found in the comparison of total fish density and total biomass. Total fish density observed during visual surveys was 50% lower than the fish density estimates obtained during seining. Total biomass estimated using visual surveys was 40% lower than total biomass estimated using the seine. The sampling strategies using by both methods may explain these differences. A maximum of 10 fish per species were noted in the visual surveys, whereas no limit in the number of fish was given for the seine. That was particularly the case for *L. gibbosus* that reached the maximum in almost every sampling site. Therefore, the theoretical maximum of fishes that could be computed within a site with the visual survey was of 70 fishes (7 species x 10 fish), while no such limit existed with the seine. Indeed, the maximum number of fishes sampled within a site was 44 individuals with the visual surveys and 190 individuals using the seine. The correlation analyses performed on the total fish density and the total fish biomass, however, indicated that although the seine captured an higher number of individuals at each site, the observations obtained by the visual surveys were significantly correlated with data collected with the beach seine. For both sampling methods, the total fish density and the total fish biomass increased as the macrophyte density increased.

The visual survey method has several advantages over seine sampling. It allows a simultaneous census of the fish community and the environmental characteristics in which the fishes are sampled (Werner et al. 1977). It is a non-destructive method which enables the observer to do repeated sampling over time (Hall and Werner 1977). Furthermore, swimmers can make observations in areas such as dense weed beds, bottoms covered with boulders, and zones affected by logging that are difficult to sample with most fishing gears (Helfman 1983). There is in practice no limit to the number of fish an observer may keep track on during visual surveys. For instance, divers studying fish communities on coral reefs register a great amount of information using visual surveys. However, error on the absolute number of fish increases as the density of fish increases and it may be useful in certain situations to use abundance classes. The probability of making mistakes in the recording of fish counts and measures increases with fish density. Furthermore, fish mortality due to the time required to manipulate the fish also increases with fish density.

Shortcomings to the visual survey method involve the physical conditions of the water and the substrate, fish behaviour, subjectivity of the observer, and meteorological conditions. The major factor which may limit the use of that method is the visibility. The sampling of lakes during phytoplankton blooms or after strong winds that charged the water with high loads of suspended solids may decrease the efficiency of visual census. Furthermore, the degree of sunlight may also affect the visibility of fish in some lakes because of the refraction of light on the suspended particles. Sampling days in this present study were chosen based on the similarity of climatic conditions precisely to avoid the influence of sunlight. Although the visibility limits the efficiency of the visual census in certain conditions, it is very difficult to define a depth limit in which visual surveys could be performed. The lowest visibility at which the visual method can be done depends greatly on the research interest. For instance, one could efficiently perform visual census in a lake with a low visibility of 1 m if the interest was to study the impact of fish grazing on periphyton growth in the littoral zone of a highly eutrophic lake. On the other hand, if the interest was on the impact of rocky substrate on the competitive interaction between two fish species, then the low visibility would likely preclude the use of visual surveys.

Chapitre 2

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

A. Brind'Amour, D. Boisclair, P. Legendre and D. Borcard

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ABSTRACT

Using a new statistical tool, *Principal Coordinates of Neighbor Matrices* (PCNM), 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 in four categories at spatial scales ranging from 2 km (very broad scale) to less than 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 may 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 single spatial scale. This study provides a quantitative support to the idea that the littoral zone of lakes may 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.

INTRODUCTION

Littoral zones represent the most diversified, productive, and heterogeneous portions of lakes (Wetzel 1990). They are characterized by a diversity of micro-habitats composed of a variety of physical and biological structures that result in complex biological interactions (Werner et al. 1977, Chick and McIvor 1994). 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 habitat may take place at different spatial scales. Hence, both the abiotic and biotic factors observable at different spatial scales may influence the structure of fish communities.

The word 'scale' has been commonly used in various contexts and with multiple meanings (Gozlan et al. 1998, Eagle et al. 2001, 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 may 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 may 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 may 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 (Syms 1995, 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 may be thought of as reflecting the perception an organism may have of its environment, rather than the perception of the investigator. Consequently, these approaches not only enhance the 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 Neighbour Matrices (PCNM), which may be used to describe the dominant spatial scales at which species are varying. In comparison to other multiscale approaches, which operate at a few selected scales, this method presents the advantage of analysing 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, may 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 the spring and summer of 2001 (Figure 2.1). 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 waterlilies *Nymphea sp.* This mesotrophic lake has a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km (calculation 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.

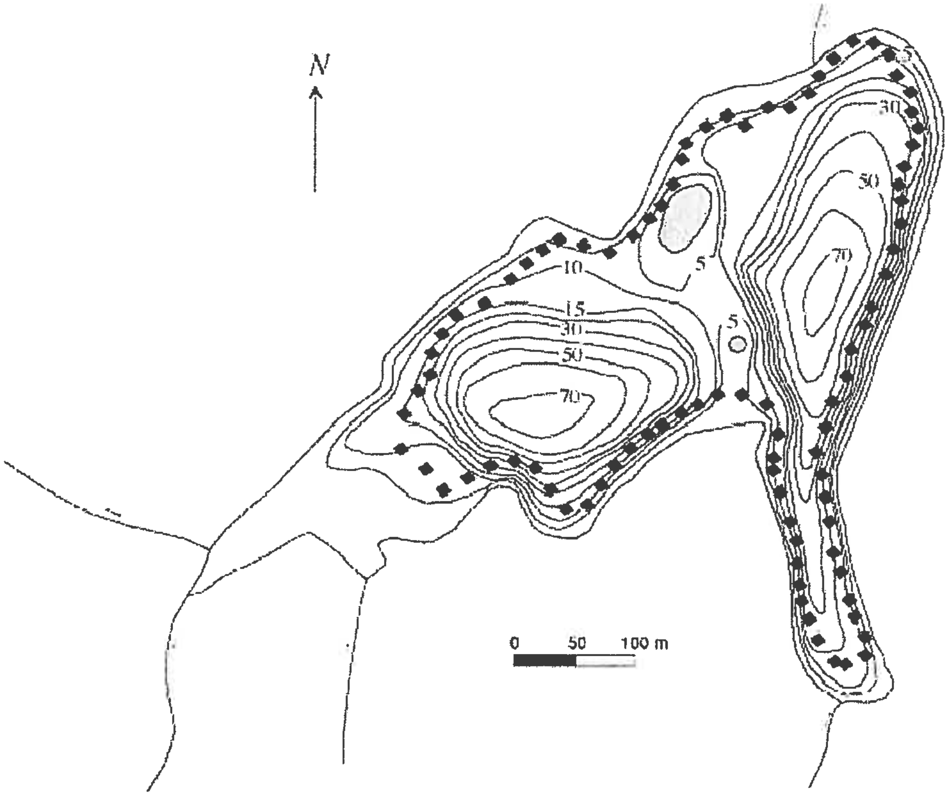


Figure 2.1 Map of Lake Drouin (Lanaudière, Québec). Black dots represent the 90 sampling sites in the littoral zone of the lake.

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 to 67.2 m). The width of a sampling site (5 to 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 to 12 m). Geographical coordinates were estimated at each site using a global positioning system (Garmin - GPS 12) with a precision of ±10 m. The perimeter of the lake was further separated in 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 may change among periods within a day (dawn, mid-day, dusk; Keast and Harker 1977). The sites were surveyed three times (i.e., on 6 consecutive days) in the spring (from 25 June to 30 June), and again during the summer (from 29 July to 04 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 the Appendix A.

Fish community sampling

Survey of the fish community was done using 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 approximately 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 min^{-1} to minimise fish disturbance (Eklöv 1997). The snorkelers noted their observations on plastic PVC cylinders. They identified the species, their relative abundances, and the approximate sizes of the fish (Table 2.1) 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 = 4-5 individuals; 5 = 6-9 individuals, and 6 = 10 individuals and more. Table 2.1 shows the species size classification that was used during the surveys.

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 based on the approach described above may be appropriate when these descriptors vary at least two-fold among the sampling sites.

Table 2.1 Species size classes used in the text. The species marked with an asterisk was excluded from the analysis because its total abundance was less than 1%. Numbers in parentheses indicate the percentage (%) of fish observed by size class.

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

Computations

The fish community at each site was characterized using three types of descriptors: the community composition, total fish density, and relative fish biomass. The total fish density was calculated by dividing the total fish abundance by the unit area of the sampling site. Since 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:

$$B = \Sigma n_{i,s} \text{ x } M_{i,s} \qquad (1)$$

where $n_{i,s}$ is the number of fish per species per size class and $M_{i,s}$ is the average fish mass (grams) per species per size class estimated using 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

Characterization of the sampling sites was done by measuring 11 environmental variables at each site: average temperature (°C), dissolved oxygen (mg L^{-1}), 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 2.2). 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^2 quadrats (a 1 m^2 frame was thrown from the center of the sampling site to different directions within each site). The number of stems from emergent and submersed species per 1 m^2 was counted. The average number of stems from the four replicates

Table 2.2 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_2	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
Warf	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

was used in the statistical analysis. The percentage cover of plants covering the substrate, including all species, 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 largest 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 non-neighboring sites by a value equal to 400 (4 x 100 m). The distance between the first and last site was also retained in order to form a closed loop which depicts the natural structure of a lake shore (Figure 2.2). The choice of that arbitrarily value was made according to a sensitivity analysis done by Borcard and Legendre (2002). They found that multiple regressions using 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 computed a principal coordinate analysis (PCoA) 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 using 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).

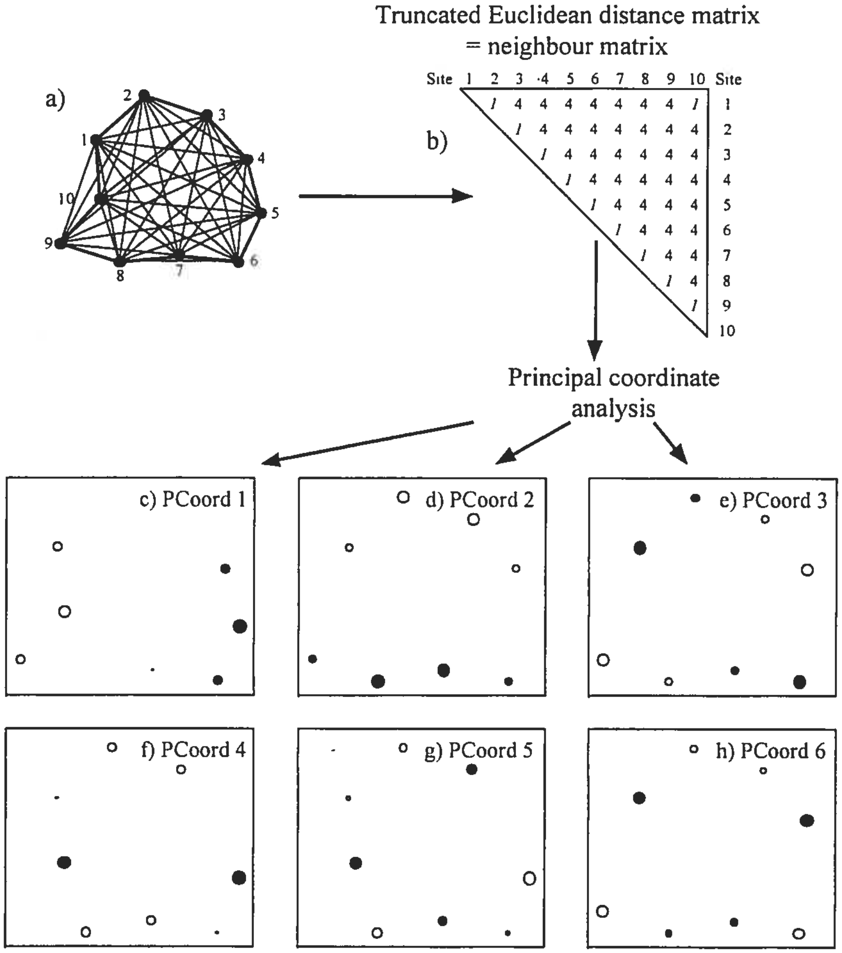


Figure 2.2 PCNM variables around a fictitious structure forming a loop. (a) Sites localized on the map. (b) Neighbor matrix. Distances between neighboring sites (heavy lines in a) are written in the neighbor matrix in b; these distances are equal to 1 in the example. Distances between non-adjacent sites (light lines in a) are replaced by 4 times the maximum value (max=1 in the example, 4 × 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.

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 using forward selection of the explanatory variables in SPSS (SPSS 1999) for the global metrics (single response variable).

PCNM variables correspond to a series of sinusoids with decreasing periods. Based on 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 analysed. 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 using 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 using SPSS (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 less than 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 (Figure 2.3A) and in August (Figure 2.3B). An exception was observed *L. gibbosus* (Legi) which displayed high densities in almost all the sites in the two sampling months. The other species as well as the total fish density and the relative fish biomass, were distributed in patches of varying sizes localised in different regions of the lake.

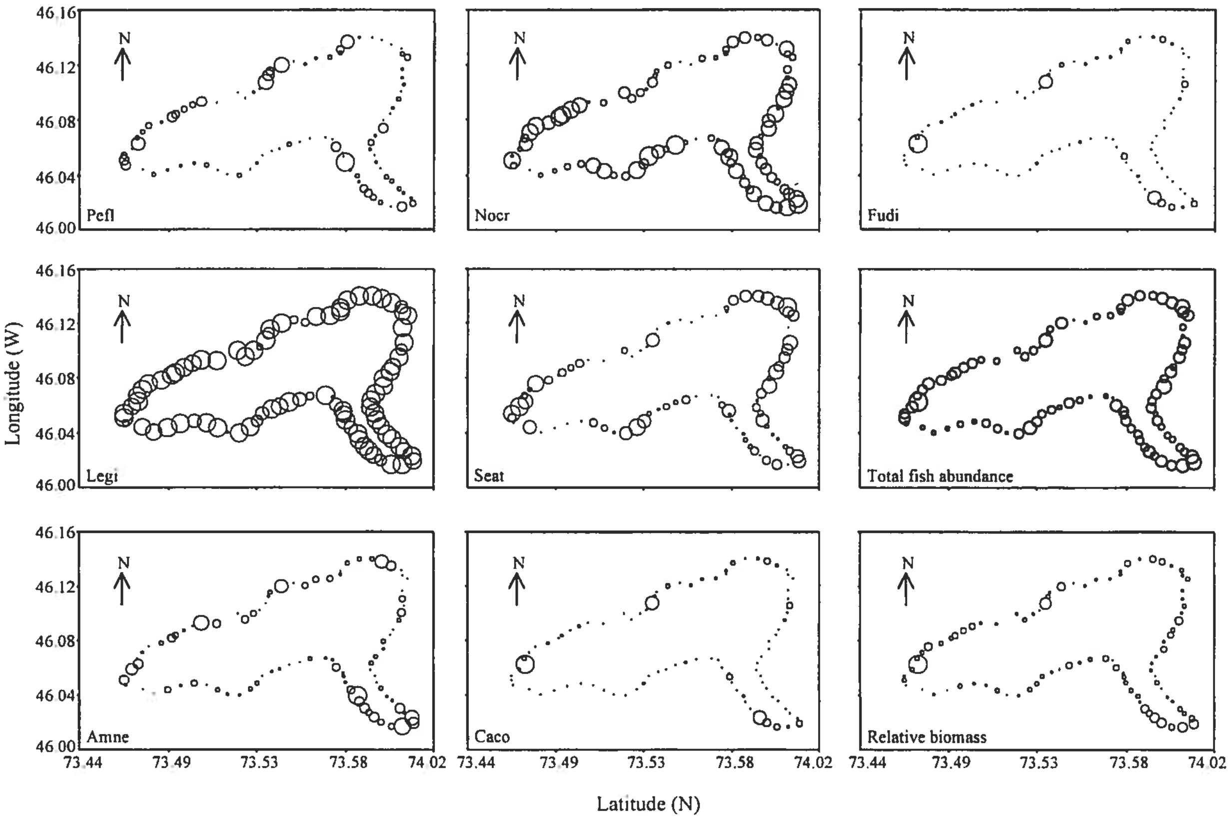


Figure 2.3A Map of Lake Drouin showing the observed values of the fish community descriptors for the month of June. The size of the bubbles is proportional to the observed values.

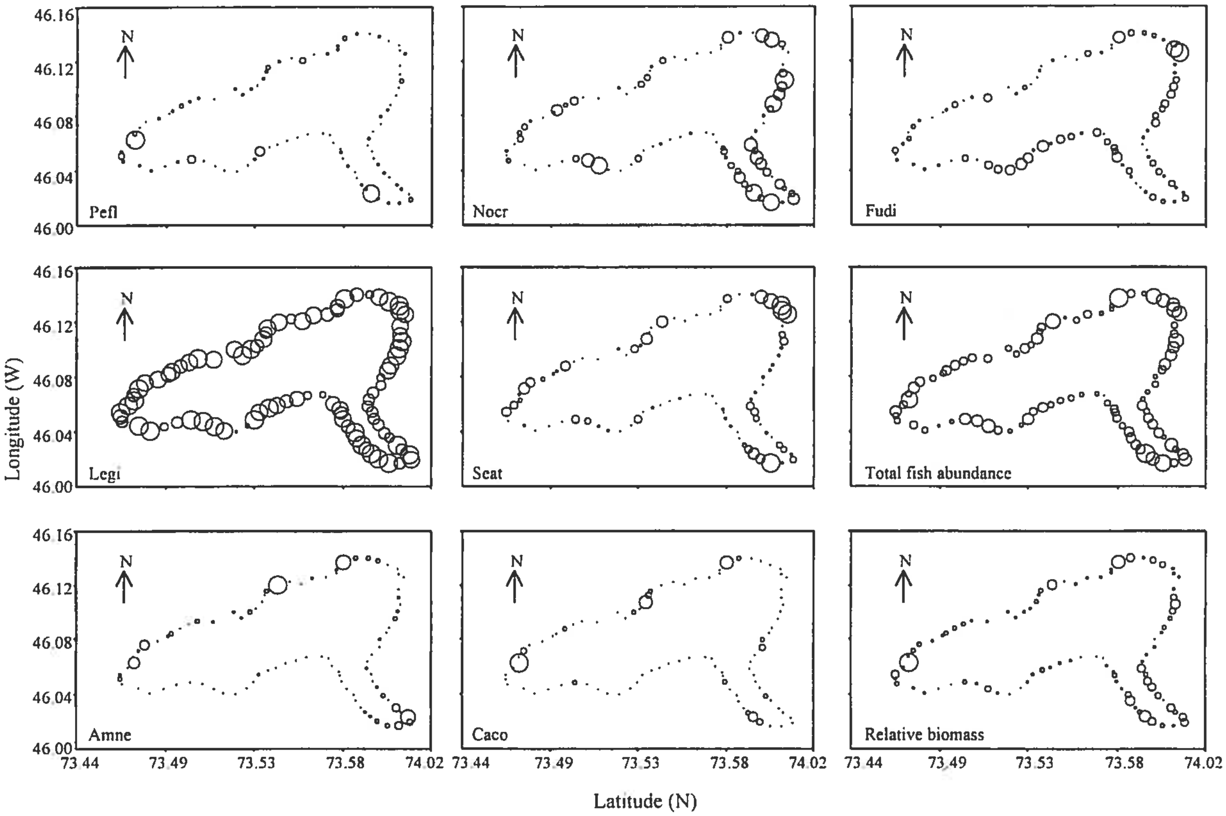


Figure 2.3B Map of Lake Drouin showing the observed values of the fish community descriptors for the month of August. The size of the bubbles is proportional to the observed values.

Classification of spatial scales

The variance of the littoral fish community was decomposed with respect to submodels of significant PCNMs. Based on the similarity of their periods, the PCNMs were grouped into four submodels: a very broad-scale submodel with a range nearly 2 km, corresponding to PCNM 1 and 2; a broad-scale submodel ranging from 500 m to 1000 m, corresponding to PCNMs 3 to 9; a meso-scale submodel ranging from 200 m to 450 m which corresponded to PCNMs 10 to 35; a fine-scale submodel with a range less than 100 m corresponding to PCNMs 36 to 60.

Multiscale patterns

June —The three descriptors of the fish community displayed spatial variability across 19 of the 60 PCNMs (Table 2.3). 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 2.4a). The density of *N. crysoleucas* was highest in the northern part of the lake (Table 2.5a; Figure 2.4a).

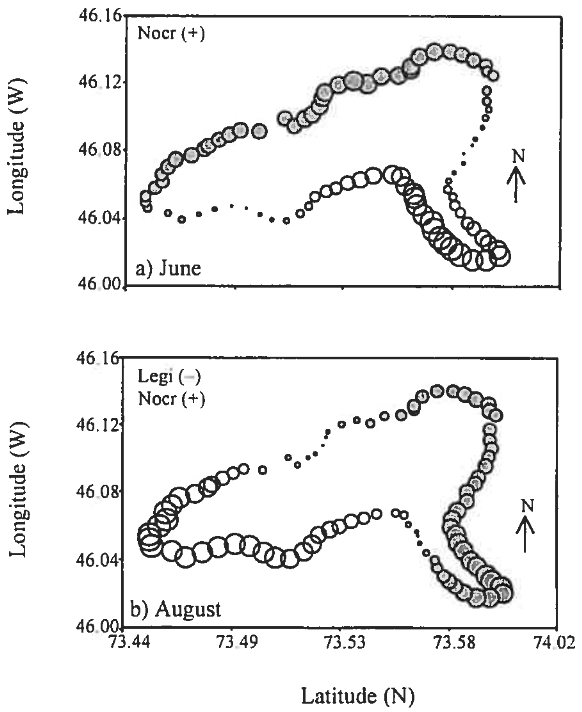


Figure 2.4 Map of Lake Drouin showing (a) the forecasted values of the community composition in June, and (b) the three fish community descriptors in August at the very broad scale (≥ 2 km). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (–) are abundant in the filled and empty bubbles respectively; see Table 4 for details. Species codes are given in Table 1.

The environmental variables explained 51% of the spatial variation in density of *N. crysoleucas* (Table 2.6). Fetch (Fet) was the explanatory variable contributing most to the model as shown by its the 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).

Table 2.3 Regression/canonical coefficients for standardized variables of fish community descriptors detected at different spatial scales in June. Column headings: coefficients of determination (R^2) for the whole spatial model.

PCNM no.	Community composition	Total fish Density	Relative fish biomass	
	R^2=0.195	0.422	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

Table 2.4 Species scores on the first canonical axis of each spatial scale submodel for the months of June and August. *: Species which are markedly contributing to a given scale. No significant relationship was found between the community composition and the fine spatial scale in August.

	Submodels			
	Very broad	Broad	Meso	Fine
(a) 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*
(b) 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	

Table 2.5 Median values of the fish community descriptors for the four submodels (a) for the month of June and (b) the month of August.

	Submodels			
	Very broad	Broad	Meso	Fine
(a) June (fish m^{-2})				
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	0.001
Total fish density		0.086	0.078	
Relative fish biomass (g m^{-2})		2.061	1.707	1.698
(b) August (fish m^{-2})				
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^{-2})	0.923	0.942	0.923	0.733

Table 2.6 June: standardized coefficients (*b*) of environmental variables which explained significant components of the spatial patterns (PCNM models) of the littoral fish community descriptors at four different spatial scales. See Table 2 for the environmental variable codes. Column headings: coefficients of determination (R^2) of the models. * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$.

	Community composition			Total fish density		Relative fish biomass		
	V. broad	Broad	Meso	Broad	Meso	Broad	Meso	Fine
R^2=	0.513***	0.263***	0.198***	0.171***	0.047*	0.363*	0.295*	0.052*
Riv		−0.247**		−0.211*		−0.409***		
Lit		−0.376***						
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								
Tree					-0.217*			
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*

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 2.5a; Figure 2.5a). 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 2.5a; Figure 2.5b). The environmental variables that significantly contributed to the broad-scale submodels were similar among the community descriptors (Table 2.6); they explained 26, 17, and 36% of the among-site variability in community composition, in total fish density, and in 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 or 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 (Figure 2.6a, b). The first distribution pattern, displayed by the community composition, consisted of patches of three species, *N. crysoleucas* (Nocr), *S. atromaculatus* (Seat), and *C. commersoni* (Caco; Figure 2.6a), that alternated with those of *L. gibbosus* (Legi) and *F. diaphanus* (Fudi; Table 2.5a). The second pattern showed patches of high forecasted

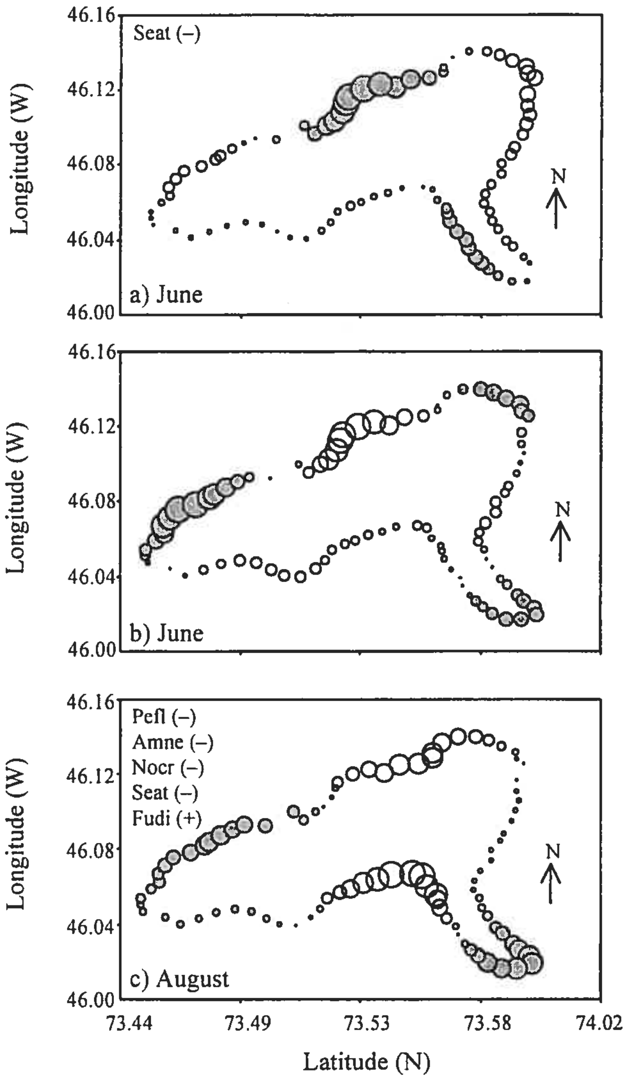


Figure 2.5 Map of Lake Drouin showing (a) the forecasted values of the community composition, and the total fish density, (b) relative fish biomass in June. (c) The community composition, the relative fish biomass and the total fish density in August at the broad scale (500-1000 m). The size of the bubbles 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.

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 2.5a; Figure 2.6b).

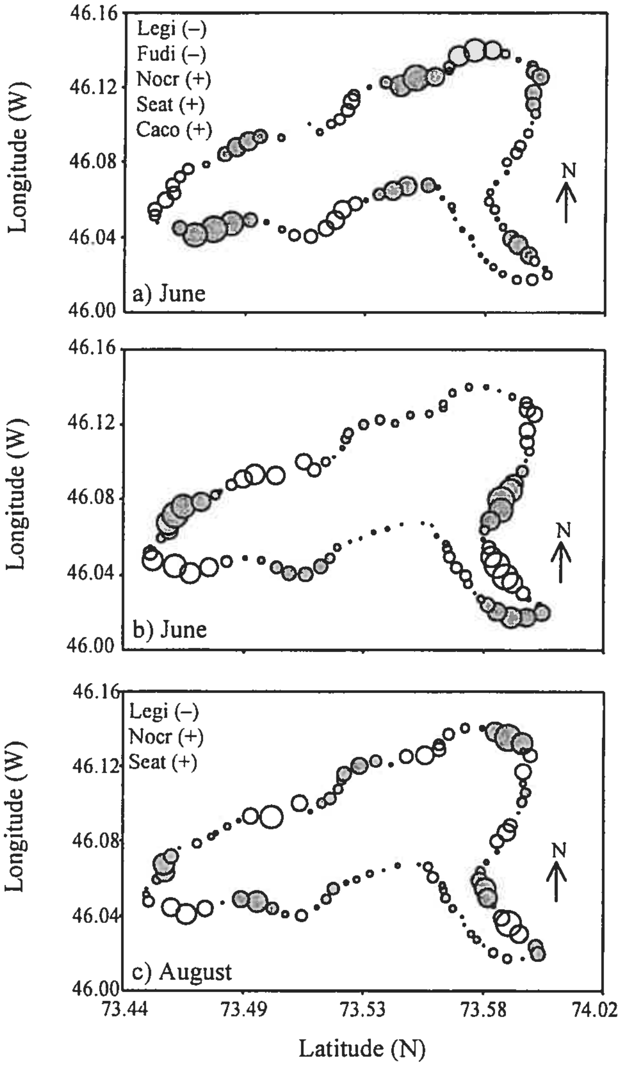


Figure 2.6 Map of Lake Drouin showing (a) the forecasted values of the community composition and the total fish density, and (b) relative fish biomass in June. (c) The three fish community descriptors in August at the meso scale (300-500 m). The size of the bubbles is proportional to the forecasted values. 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.

The environmental variables (Table 2.6) 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 bottom cover by macrophytes (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 (Tree: b=–0.217).

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 (Figure 2.7a; Table 2.5a). 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 2.6), 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 2.7). 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 very broad-scale to fine-scale.

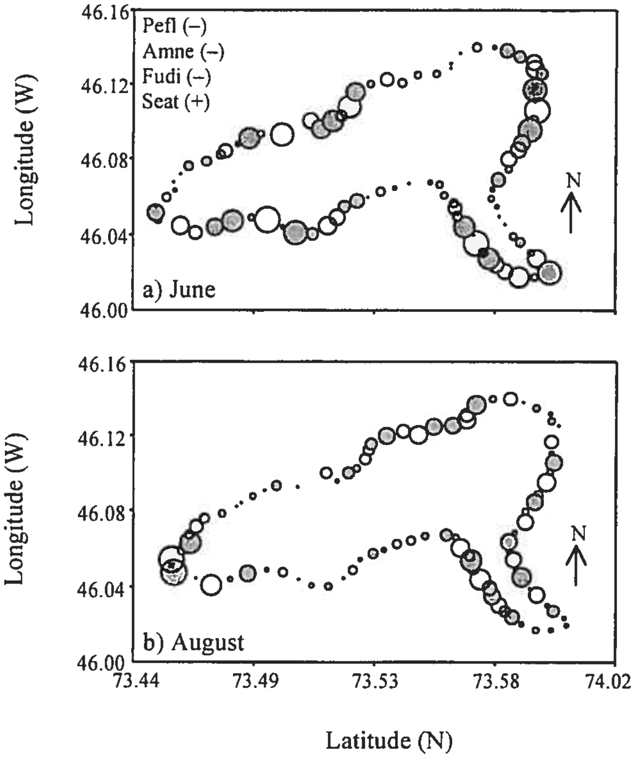


Figure 2.7 Map of Lake Drouin showing (a) the forecasted values of the community composition and the relative fish biomass in June . (b) The total fish density and the relative fish biomass in August at the fine scale (<100 m). The size of the bubbles is proportional to the forecasted values. The species marked with (+) and (–) are abundant in the filled and empty bubbles respectively; see Table 4 for details. Species codes are given in Table 1.

Similar patterns of spatial variability of the community composition, total fish density, and relative fish biomass were observed at very broad scale (Figure 2.4b; Table 2.5b). Species scores indicated that the abundance of *L. gibbosus* (Legi) was more abundant along the eastern part of the lake (Table 2.4). 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 (Figure 2.4b). High proportions of the variability of community descriptors were explained by the environmental variables (Table 2.8, community 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 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 tree (Tree), density of emergent macrophytes (Emer), riparian slope (Riv), and sand as substrate (S1).

Similar patterns of spatial variability of the community composition, total fish density, and relative fish biomass were observed at broad scale in August (Table 2.7). Four species were distributed along the northern and southern parts of the lake (Table 2.4b and Figure 2.5c): *P. flavescens* (Pefl), *A. nebulosus* (Amne), *N. crysoleucas* (Nocr), and *S. atromaculatus* (Seat). *F. diaphanus* (Fudi; Table 2.5b) 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 2.8). 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 density 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.

Table 2.7 Regression/canonical coefficients for standardized variables of fish community descriptors detected at different spatial scales in August. Column headings: coefficients of determination (R^2) for the whole spatial model.

PCNM no.	Community composition	Total fish abundance	Relative fish biomass	
	R^2=0.231	0.483	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

Table 2.8 August: standardized coefficients (*b*) of environmental variables which explained significant components of the spatial patterns (PCNM models) of the littoral fish community descriptors at four different spatial scales. See Table 2 for the environmental variable codes. Column headings: coefficients of determination (R^2) of the models. * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$.

	Community composition			Total fish density			Relative fish biomass		
	V. broad	Broad	Meso	V. broad	Broad	Fine	V. broad	Broad	Meso
R^2=	0.720***	0.140***	0.130**	0.760*	0.289**	0.047*	0.760*	0.331*	0.152***
Riv				0.126*			0.126*		
Lit									
Z									
S1				0.109*			0.109*		
S3								−0.316**	
S4		−0.373*			−0.420***			−0.536***	
S8					0.279**				
U1									
U2									
U3						0.217*			
U4									
U5									
Tree	−0.197**		0.209*	−0.194***			−0.194***	−0.215*	0.389***
Emer	−0.267***			−0.160**			−0.160**		
Cov	−0.177**		−0.263**					−0.250**	
Fet	−0.749***			−0.802***			−0.802***		
Trib									

At meso scale, the community descriptors displayed a pattern of variation consisting of patches ranging from 100 m to 500 m along the shore (Figure 2.6c; Table 2.5b). The species scores indicated that *L. gibbosus* (Legi) and *N. crysoleucas* (Nocr) were both distributed inversely to *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 2.8). The submodel of the relative fish biomass was explained by the presence of riparian trees (Tree: b=0.389). Bottom cover by macrophytes (Cov: b=0.263) and riparian trees (Tree: b=–0.209) 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 (Figure 2.7b; Table 2.5b). 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 2.8).

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 2000 m), a broad scale (from 500 m to 1000 m), a meso scale (from 200 m to 450 m), and a fine scale (<100 m). Following the hierarchy theory of Allen and Starr (1982), our study suggests that Lake Drouin may be primarily structured by the fetch, a very broad-scale physical process. Through energy inputs, fetch may 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 2.9) 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 (Syms 1995, Eagle et al. 2001, Gust et al. 2001, Wilson 2001) and rivers (Poizat and Pont 1996, Lohr and Fausch 1997, Magalhaes et al. 2002). 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). Since our study covered the complete perimeter of the littoral zone using 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 to 0.75) and to a lesser extent emergent macrophytes (b=0.28 to 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 may influence fish community in several ways.

Table 2.9 Habitat classification based on the environmental variables associated with the four spatial submodels.

Spatial scale	Theme	Habitat characteristics	Subclass	Description
Very broad (~ 2000 m)	Exposed emergent	Wave exposure	High	Fetch: 340 – 1406 m
			Low	Fetch: 0.00 – 340 m
		Emergent macrophyte	High	Emergent (June) > 8.50 stems m^{-2}
				Emergent (August) > 42.75 stems m^{-2}
Broad (500–1000 m)	Heterogeneous substrates	Littoral slope	Low	Mean of 0.28
		Substrates	Rocky	Rocks and boulders 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%)

According to Nixon (1988) and Randall et al. (1996), fish production (kg ha^{-1}) and fish abundance may 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 the biomass of benthic organisms (Burkholder 1992), which may provide food resources for the fish. Fetch may also indirectly affect macrophyte growth, which can in turn procure refuges to certain fish species. Intermediate fetch has a positive effect on macrophytes growth (Keddy 1983) and, as several studies have shown, macrophytes positively affect the density of littoral fish within a lake (Laughlin and Werner 1980, Hinch and Collins 1993, Chick and McIvor 1994, Weaver et al. 1997). 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. Since we sampled the macrophytes and the fetch on only two occasions within each season, we may not have covered a sufficient temporal scale to observe any potential positive relationship.

Habitats at broad scale (500 to 1000 m) were composed of heterogeneous physical substrates ranging from rocks and boulders (b=0.21 to 0.54) to woody debris (b=0.28) and low littoral slopes. Studies in lakes with limited growth of macrophytes have showed that rocky and woody substrates have the same ecological importance as macrophytes in structuring fish communities (Beauchamp et al. 1994, Falcon et al. 1996, France 1997). 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 in 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 to 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, Stauffer et al. 2000). 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 into 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 may 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 may 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. Other 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 (Ricklefs 1987, Pinel-Alloul et al. 1999). Results at finer scales could also be explained by our sampling strategy. We may not have adequately measured abiotic variability occurring at the finer spatial scales (Weaver et al. 1996, Jackson et al. 2001). For instance, some fish may 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 to June, the environmental variables explained a higher proportion of the variance of the fish community descriptors in August. This was particularly apparent for the broader spatial scales where the difference reached almost 25%. This result could be explained by the fact that the littoral zones of lakes are more physically structured in late summer than in the spring. Macrophyte growth in north temperate lakes reaches its maximum in August; this was also observed in our study where the density of emergent macrophytes was more than twice as high in August (average: 7.50 ± 12.70 stems m^{-2}) than it was in June (average: 3.25 ± 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). Since different features of habitats may 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; Figure 2.8). 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. Based on the scale dependency that species displayed, we identified two functional groups in Lake Drouin. The first functional group, the cyprinids and small-sized species (*N. crysoleucas*, *S. atromaculatus*, and *F. diaphanus*) were either associated with a wide range of spatial scales (from 450 m to 2 km) or to 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.

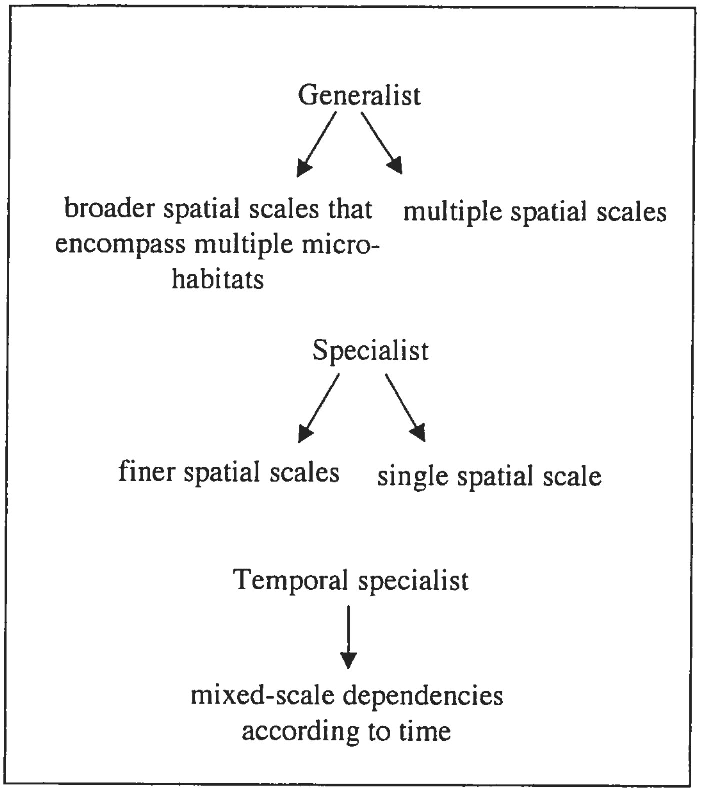


Figure C.1 Schéma de la distribution des groupes fonctionnels basé sur l'association des espèces avec l'étendue d'utilisation des échelles spatiales

This is supported by our results since *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 substrates (Crowder and Cooper 1982, 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 utilize 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 may preclude competition and favor coexistence between species (Werner and Hall 1976, Laughlin and Werner 1980). 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 behaviour. The black bullhead is a chemo-sensory 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 may utilise the same habitat, feeding at different times of the day.

Temporal specialisation 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 may 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 may be preferable to a single-scale approach. From a management perspective, the statistical method applied in our study may help delineate units of conservation for which management actions could be developed, in order 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 community 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 may present a framework for future development of fish habitat models based on the spatial scales at which the fish are responding. It is tempting to speculate that habitat models based on variables associated with different spatial scales may improve the predictions of fish-habitat relationships because these models integrate much more information on different habitat requirements of fish species.

APPENDIX A

This appendix justifies (i) the combination of two one-day surveys to get one full survey around the perimeter of the lake and (ii) the pooling of three consecutive perimeter surveys into a single summed survey around the lake. The justification of the combination of the two one-day surveys was done using non-parametric multivariate analysis of variance (MANOVA) with a two-way crossed variable design (see (Anderson 2001). The rationale for analyses of variance was to test the hypothesis that all the surveyed days came from the same statistical population. The dependent variables were all included in a matrix containing the standardized community descriptors (abundances per species, total fish abundance, and total biomass). The main factors in these analyses were the survey days (Day) and the section of the lake (Section). The non-significant effect of the day (D) or the interaction Day x Section justified our pooling of the data from two consecutive days (Table A.1). Separate analyses were done for the two survey months (June and August).

Justification for pooling of three consecutive perimeter surveys was obtained using a test of congruence among distance matrices (CADM, (Legendre and Lapointe 2004). This test was designed to verify if two or more data matrices can be combined in view of a joint analysis. Since the CADM test requires distance matrices, we transformed our three tables containing community composition data for each perimeter into Hellinger distance matrices (Legendre and Legendre 1998). The test verifies i) that the matrices are congruent and ii) that they are correlated. The congruence is tested using the Friedman chi-square statistic, whereas the correlation among matrices is tested using the Mantel statistic. Rejection of the null hypothesis (H_0 : all matrices are incongruent; Table A.2) and significant correlations among the matrices (Table A.3) were interpreted as justification to pool the three consecutive perimeter surveys. These analyses were carried out separately for each survey month (June and August).

Table A.1 Results from the non-parametric Multivariate Analysis of Variance based on 999 permutations.

Source	df	F	*P*
June			
Day	2	1.383	0.344
Section	1	0.097	0.890
Day*Section	2	1.204	0.344
August			
Day	2	0.569	0.701
Section	1	0.979	0.443
Day*Section	2	1.361	0.241

Table A.2 Justification for pooling the matrices, obtained by the CADM test which uses the Friedman chi-square statistic computed for distance matrices. Test results are based on 999 permutations.

	Statistic	*P*
June		
Friedman chi-square	5220.613	0.001
August		

Friedman chi-square	5550.189	0.001

Table A.3 Mantel correlations among the three perimeter survey distance matrices. The associated probabilities, based on 999 permutations, are in parentheses.

	Matrix 1	Matrix 2	Matrix 3
June			
Matrix 1	1.000	0.152 (0.001)	0.123 (0.002)
Matrix 2	0.152 (0.001)	1.000	0.180 (0.001)
Matrix 3	0.123 (0.002)	0.180 (0.001)	1.000
August			
Matrix 1	1.000	0.236 (0.002)	0.206 (0.002)
Matrix 2	0.236 (0.002)	1.000	0.138 (0.015)
Matrix 3	0.206 (0.002)	0.138 (0.015)	1.000

Chapitre 3

Multi-scale assessment of the functional relationship between species traits and environmental conditions for littoral fish communities

A. Brind'Amour, D. Boisclair, S. Dray et P. Legendre

En préparation

ABSTRACT

We assessed the relationship between fish spatial distributions, fish morphological and behavioral traits, and habitat characteristics in the littoral zone of two Canadian Shield lakes across multiple spatial scales. Our results showed that the fish communities were spatially structured along the vertical (water column) and horizontal (habitats) dimensions. We observed concordance among the species traits, suggesting the presence of three functional groups of species according to the positions of the mouths and the locations of the fish in the water column (superior-surface, terminal-mid-water, and inferior-benthic). Species traits within a same functional group varied similarly with habitat conditions, suggesting the presence of spatially structured ecomorphological relationships. Habitat conditions varied across spatial scales and the relationships between functional groups of species and their environment were found to be scale-dependent. For instance, habitat depth, density of macrophytes (emergent and submersed), rocky and woody substrates were significantly discriminating variables among the functional groups at very broad spatial scale. Emergent macrophytes and rocky substrates were contributing most to discriminate the functional groups at broad scale. Interpretation of these trait-habitat relationships was restrained, however, by the low values of the correlation coefficients, which ranged from 0.057 to 0.197. Nevertheless, our study represents a quantitative contribution to the detection of mechanisms potentially explaining the scale-dependent influence of environmental complexity on the community organization of littoral fish in lakes. From a management perspective, development of fish-habitat relationships based on species traits is increasingly appealing, because

different lakes differ in species composition, but they may share similar functional groups of species.

INTRODUCTION

Prediction of fish species distributions is of primary importance in ecology and conservation biology, and reliable predictive models are increasingly needed because of habitat loss and modification. The diversity of species compositions among lakes and the multitude of species responses to the spatially structured littoral zones highlight the complexity of ecological fish habitat modeling (Brind'Amour et al. 2005). Functional classifications of species into groups sharing similar traits may help circumvent the challenges of modeling fish communities as such analyses can provide useful information on the internal functioning and hierarchical structure of fish communities (Kneitel and Chase 2004). Functional groups may also be used to simplify complex ecosystem models by reducing them to an ecologically meaningful level of complexity (Nagelkerken and van der Velde 2004). For instance, assemblages of fish species sharing similar traits form operational units responding to environmental changes in a more predictable manner than individual species (Austen et al. 1994). Development of fish-habitat relationships based on species traits would likely enhance the transferability of models among lakes, because different lakes may differ in species composition, but they may share similar functional groups of species (Angermeier and Winston 1998).

Functional relationships relating the species traits to their environment rely principally on the ecological niche concept (Hutchinson 1953); utilization of resources by a species, within a particular habitat, is primarily constrained by or should correlate with its morphological traits (Gatz 1979a). In such a manner, habitats may be viewed as filters imposed on a species pool to select species traits suited to a particular set of environmental conditions (Keddy 1992). These filters, representing abiotic or biotic selective forces, act through deletion, removing species not adapted to the local conditions (Díaz et al. 1998). Hence, habitat acts as a template on which evolution forges life-history strategies (Southwood 1977, 1988). The strategies used by a species to increase its fitness in a given location thus depend on the morphological and physiological constraints arising from its phylogenetic history. Species sharing similar traits will likely converge into similar habitats, even if they are found in distant regions (Lamouroux et al. 2002).

Responses of fish species to habitat heterogeneity are increasingly examined in a hierarchical spatial context (Allen and Starr 1982, Kolasa 1989). For instance, Tonn et al. (1990) provided a spatial framework in which a series of environmental filters acting on continental, regional, and local fish species determined the species composition within lakes. Brind'Amour et al. (2005) recently observed that the spatial distributions of littoral fish species, within a lake, were both habitat- and scale-dependent. Because the strength of the relationship between littoral fish species and their habitats depends not only on the nature of the environment (i.e. habitat conditions) but also on the spatial scale at which the relationship is observed (Poizat and Pont 1996, Brind'Amour et al. 2005), functional classifications of species within lakes should thus be studied across a wide range of spatial (and/or temporal) scales (Wiens 1976, Menge and Olson 1990).

To be useful, functional classifications must be defined by fish species traits that best explain the responses of species (e.g. species abundances) to environmental variability (Nygaard and Ejrnaes 2004). This is rarely done because no standard statistical method allows the analysis of the relationship between these three components simultaneously (i.e. species traits, response of species, and environmental conditions). Legendre et al. (1997) developed a three-matrix approach, the so-called fourth-corner method, that allows for the significance testing of species traits-environment correlations based on information from the table of species traits, the table of species abundances, and the table of environmental conditions.

In this study, we used the fourth-corner method to verify if behavioral and morphological traits determined the spatial distributions of littoral fish species in two Canadian Shield lakes. Specifically we verified 1) the presence of functional groups obtained by the association among the species behavioral and morphological traits, 2) that the species traits within a functional group vary similarly with habitat conditions, and 3) that these species traits-environment correlations vary across spatial scales, i.e. are scale-dependent.

MATERIALS AND METHODS

Study lakes

The fish communities of Lac Drouin and Lac Paré were used in this study. The two lakes are located on the Canadian Shield in the province of Québec, Canada (Figure 3.1a and 3.1b). Lac Drouin (46°09' N, 73°55'W) has a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km (calculation based on the sum of the lengths of our sampling unit). Lac Paré (46°08' N, 73°54'W) is located in the same catchment basin as Lac Drouin and has a surface area of 23 ha, a maximum depth of 9 m, and a perimeter of 3.1 km. Both lakes presented a diverse littoral zone with woody debris, rocky substrate, sandy beaches, and patches of macrophytes of mixed species such as *Brasenia schreberi*, *Eriocaulon aquaticum*, *Myriophyllum spicatum*, and *Nymphea sp*. They are both mesotrophic lakes, possessing similar limnological and geomorphological characteristics. During the period of thermal stratification (May to October), surface water temperatures range from 15°C to 26°C and bottom temperatures range from 4°C to 8°C. The thermoclines formed at 4.5 m depth in mid-June and break down in early October.

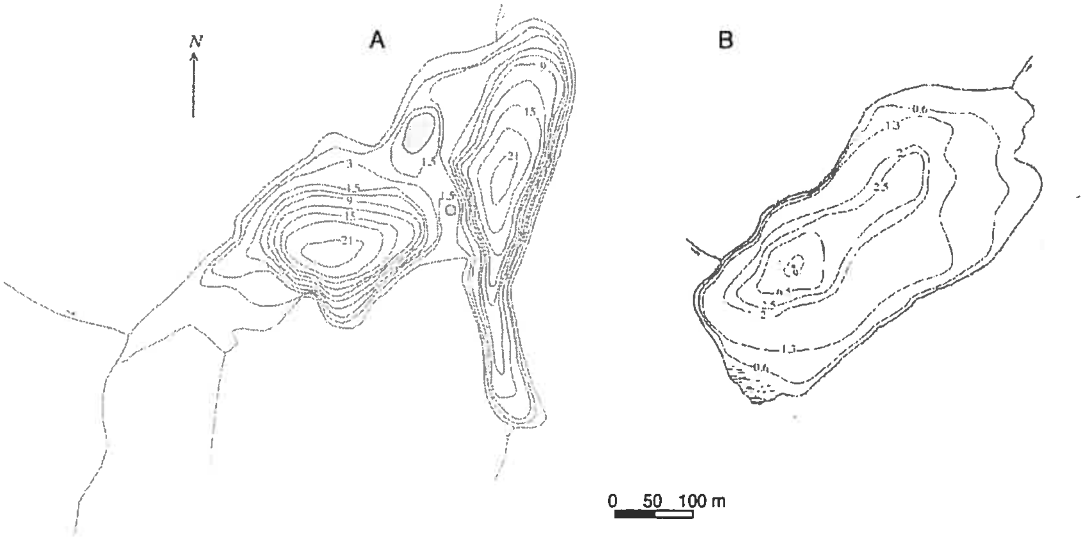


Figure 3.1 Bathymetric maps of (A) Lac Drouin and (B) Lac Paré located on the Canadian Shield in Québec (Canada).

Sampling procedure

We quantified the fish community and the environmental variables at 90 and 60 sites that covered the complete perimeter of the littoral zones of Lac Drouin and Lac Paré, respectively. The surface area of individual sampling sites ranged from 162.4 to 268.8 m^2 (average size 215.6 m^2) in Lac Drouin and from 109.2 to 390.8 m^2

(average size 207.6 m^2) in Lac Paré. Variation in the surface areas of the sampling sites was due to the fact that sites were delimited to possess fairly homogenous attributes with respect to a combination of environmental variables (i.e. substrate, macrophyte density). The width of a sampling site (5 to 10 m) was determined as 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 species while snorkeling. The mean width of a site was 10.5 m (range: 9 to 12 m) for the two lakes. Geographical coordinates were determined at each site using a global positioning system (Garmin - GPS 12) with a precision of ± 10 m.

Methodological framework

To verify if behavioral and morphological traits determined the spatial distributions of the littoral fish species in the two studied lakes, we used a modified version of the fourth-corner method (Legendre et al. 1997). This approach requires multiple data sources displayed in three different matrices (Matrix **A**, **B** and **C**) to compute species traits-environment correlations in a fourth matrix (Matrix **D**) (Figure 3.2). This section presents the information contained in each matrix used in the fourth-corner method and describes the field methods used to collect that information.

Matrix A: Abundance of fish species.— The first matrix (**A**: kxm) contained the abundances of the k species at the m sampling sites. Survey of the fish community was done using a modified version of the visual survey technique described by Harmelin-Vivien et al. (1985). The sites from both lakes were surveyed three times (i.e. on three consecutive days) during the summer 2001, from 25 July to 4 August. The technique is fully detailed in Brind'Amour and Boisclair (2004).

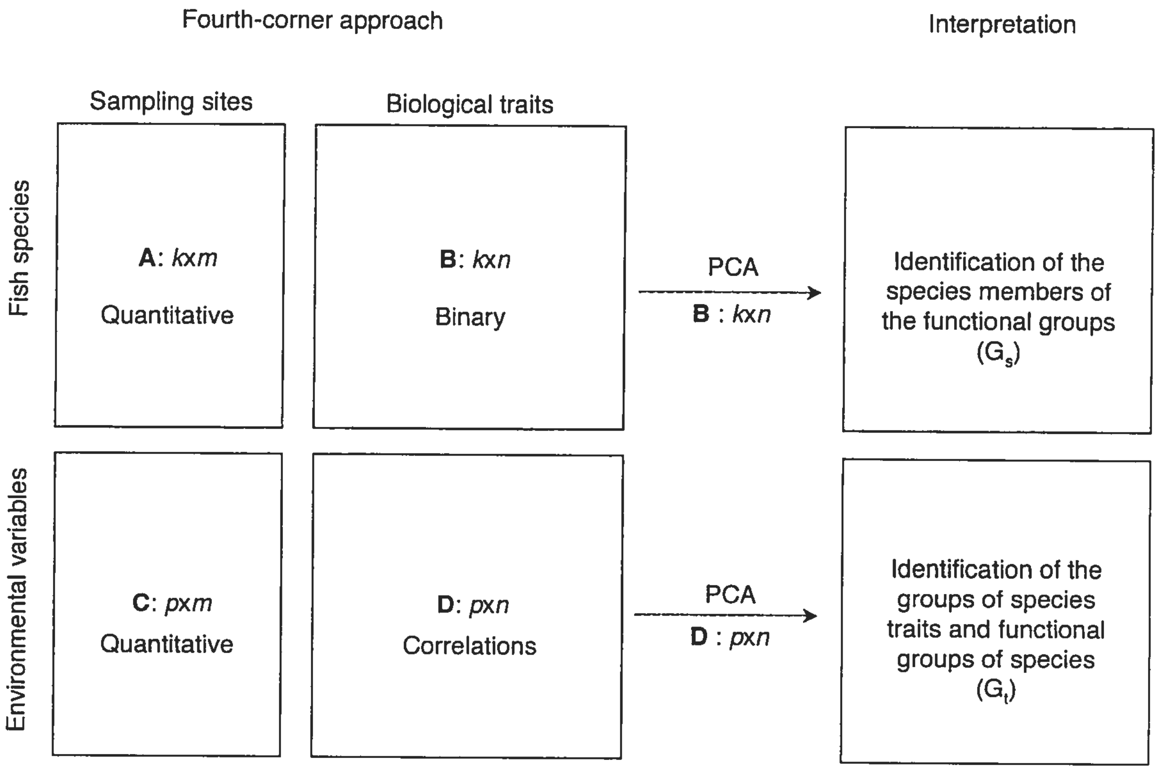


Figure 3.2 Schematic illustration of the fourth-corner statistical analysis used in our study. In matrix C, the variables are predicted values from multiple regressions (see *Materials and methods*).

Fish species, relative abundances, and the approximate sizes of the fish were estimated visually at each sampling site. Each fish was categorized according to its size: SC_1 = shorter than 110 mm total length (L_T); SC_2 = 110-160 mm L_T; SC_3= longer than 160 mm L_T. We recorded a total of nine species in the two lakes: 8 in Lac Drouin and 6 in Lac Paré (Table 3.1). Pumpkinseed (*Lepomis gibbosus*) represented 51% of the fish surveyed, whereas seven species representing each less than 20% of the observations were: golden shiner (*Notemigonus crysoleucas*), creek chub (*Semotilus atromaculatus*), banded killifish (*Fundulus diaphanus*), brown bullhead

(*Ameiurus nebulosus*), yellow perch (*Perca flavescens*), lake chub (*Couesius plumbeus*), and while sucker (*Catostomus commersoni*). The fathead minnow (*Pimephales promelas*), representing less than 1% of the observed fish, was excluded from the analyses.

Table 3.1 Species size classes and composition (presence-absence) in Lac Drouin and Lac Paré . The species marked with an asterisk was excluded from the analysis because its total abundance was less than 1%.

	L_T (mm)		Lake	
Species	Small	Large	Drouin	Paré
Ameiurus nebulosus (brown bullhead)	50 – 109	110 –190	1	1
Catostomus commersoni (white sucker)	55 – 159	160 – 320	1	1
Couesius plumbeus (lake chub)	45 – 69	70 – 105	0	1
Fundulus diaphanus (banded killifish)	55 – 64	65 – 85	1	0
Lepomis gibbosus (pumpkinseed)	30 – 109	110 – 195	1	1
Notemigonus crysoleucas (golden shiner)	65 – 109	110- 225	1	0
Perca flavescens (yellow perch)	55 – 109	110 – 230	1	1
*Pimephales promelas** (fathead minnow)	≤ 40	41 – 90	1	1
Semotilus atromaculatus (creek chub)	55 – 69	70 –135	1	1

Since morphological traits and feeding behavior are expected to change with fish size (Magnan and FitzGerald 1984, Werner and Gilliam 1984), we described the fish community using two size classes per species. Therefore, matrix **A** was composed of 14 descriptors (i.e. 7 species x 2 size classes) at 90 sampling sites in Lac Drouin, and 11 descriptors (i.e. 6 species x 2 size classes, except for large brown bullheads that were not observed) at 60 sampling sites in Lac Paré. The data were transformed using the square root transformation to dampen the effects of the dominant species (Sokal and Rohlf 1995).

Matrix B: Morphological and behavioral traits.— The second matrix (**B**: *k*x*n*) described *n* behavioral or morphological traits of the same *k* species. Data in that matrix was obtained from several studies giving information on the fish species present in the two studied lakes (Scott and Crossman 1973, Becker 1983, Carlander 1997, Ultsch et al. 1999, Robb and Abrahams 2002). The species were described using eight morphological and behavioral traits (Table 3.2) that had been found to be significantly associated to the environmental conditions in other studies. Some of the trait states were not mutually exclusive; a species could be coded as feeding on several types of diet at different water levels, or living in two temperatures or dissolved oxygen classes.

Matrix C: Environmental variables.— To quantify the functional relationships between the species traits and the environmental variables over multiple spatial scales, we described the environmental variations at four spatial scales and calculated four matrices **C**, one for each spatial scale. The matrix **C** (*p*x*m*) contained information about the *p* environmental variables that were significantly associated with the *m* sampling sites at each spatial scale, as described further below. Characterization of the sampling sites was done by measuring eight environmental variables at each site (Table 3.3). All the environmental variables, with the exceptions of density of macrophytes and fetch, were surveyed at the end of May 2001.

Table 3.2 Description of the species biological and behavioral traits used in this study. Codes for the species traits are in brackets.

Species traits	
Type of diet	Plant (1)
	Zoobenthos (2)
	Zooplankton (3)
	Insect larvae (4)
	Fish (5)
Feeding level	Benthic (6)
	Water column (7)
	Surface (8)
Body morphology	Fusiform (9)
	Compressed (10)
	Cylindrical (11)
Migration	Daily (12)
	Seasonal (13)
Mouth position	Inferior (14)
	Superior (15)
	Terminal (16)
Temperature	1: 10-15°C (17)
	2: 15-20°C (18)
	3: 20-25°C (19)
Dissolved oxygen	1: 7-8 mg L^{-1} (20)
	2: 5-7 mg L^{-1} (21)
	3: < 2 mg L^{-1} (22)
Activity	Diurnal (23)
	Nocturnal (24)

The density of macrophytes was estimated on 29 July in Lac Drouin and on July 27 in Lac Paré. The density of macrophytes at each site was estimated by two snorkelers using four selected 1 m^2 quadrats (a 1 m^2 frame was thrown from the centre of the sampling site in different directions within each site). The number of stems of emergent and submersed species was counted in the 1-m^2 frame. The average number of stems from the four replicates was used in the statistical analysis. The percentage of cover (mainly composed of a dense weed bed of *M. spicatum*) was estimated and used as the bottom cover variable. Fetch was calculated on each sampling day as the distance to the shore in the direction of the prevailing wind.

Table 3.3 Numerical resolutions and codes of the environmental variables.

Environmental variable	Code	Numerical resolution
Average littoral slope	Lit	Quantitative
Average depth	Z	Quantitative
Substrates		
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
Riparian trees	Tree	Presence/absence
Riparian slope	Rip	Presence/absence
Macrophytes		
Average density of emergent	Emer	Quantitative
Average density of submersed	Sub	Quantitative
Bottom cover	Cov	Percentage

Environmental variable	Code	Numerical resolution
Spatial arrangement		
Fetch (m)	Fet	Quantitative
Distance to tributary (m)	Trib	Quantitative
Surface area of a sampling site	Size	Quantitative

Using the *Principal Coordinates of Neighbor Matrices* (PCNM) method (Borcard and Legendre 2002, Borcard et al. 2004), we decomposed the variation in the abundances of the fish community into four spatial scales (very broad, broad, meso, and fine), see Brind'Amour et al. 2005 for further details. The very broad scale corresponded to patches of nearly 1800-2000 m in shore length (i.e. ~ 40% of the total perimeter of each lake), the broad scale corresponded to patches of 500-1000 m (i.e. 10-20% of the total perimeter), the meso scale corresponded to patches of 200 to 450 m (i.e. 5-10% of the total perimeter), and the fine scale corresponded to patches smaller than 100 m (i.e. < 5% of the total perimeter).

The associations between the environmental variables and the spatial scales were computed using either multiple regressions for the quantitative continuous variables, or logistic regressions for the binary variables. The environmental variables were used as the response variables and the PCNM base functions pertaining to each spatial scale served as the independent variables. The predicted values (from the quantitative variables) or the probabilities (from the binary variables) at each sampling site, which were the relevant information, were written to matrix **C**. Therefore, matrix **C** was composed of the environmental conditions weighted by the predicted values associated to each spatial scale. The multiple and logistic regressions were computed using the R software (Team 2004).

Matrix D: Species traits-environment matrix.— Matrix (**D**: *pxn*) contained the results obtained after conducting the fourth-corner method (Legendre et al. 1997). It was composed of correlations of the *n* biological or behavioral traits crossed with the *p* environmental variables. We conducted four analyses, one at each spatial scale (i.e. four **C** matrices). Analyses were conducted using a new program, written by S.D. in the R language for this project, implementing the fourth-corner method (Team 2004). We modified the program of Legendre et al. (1997) because we wanted to use species abundances instead of presence-absence data in matrix **A**, the later being the only type of data used in the original fourth-corner program of Legendre et al. (1997). The correlations obtained in individual cells (*d*) of the **D** matrices were tested using 999 permutations, thereby producing *p* values. Holm's procedure (Holm 1979) for adjustment of multiple simultaneous tests was applied. After adjustment, only correlations remaining significant at the 0.05 level were used for ecological interpretation.

Interpretation of Matrix D.— To identify associsations of species traits, we performed a principal component analysis (PCA; Legendre and Legendre 1998) on matrix **D**. We visually identified associations of species traits in plots of the first two principal dimensions using the PCA and we validated our results with the identification of clusters of species traits using *K*-means partitioning. This clustering method uses an objective function, the total error sum of squares (TESS), and searches for the groups that minimize TESS (Legendre and Legendre 1998). Having run K-means for various numbers of groups, we used the Calinski-Harabasz criterion to decide on the best number of groups, in the least-squares sense (Calinski and Harabasz 1974; Milligan and Cooper 1985). To facilitate the interpretation of these newly formed groups, we identified species members in each of the groups using a PCA on matrix **B**.

Global statistic.—A global statistic estimating the overall significance of the correlations in matrix **D** was calculated at each spatial scale. That statistic represented the total variability of the species traits explained by the environment and it was calculated using canonical redundancy analysis (RDA; Rao 1964). The information found in the three matrices (**A**, **B**, and **C**) described in the previous paragraphs was used in the RDA. Precisely, the product of matrices **A** and **B'** represented the species behavioral and morphological traits weighted by the species abundances. We used this product (**AB'**) as the matrix of responses variables in RDA and the matrix **C** (i.e. the environmental conditions at each spatial scale) was used as the matrix of explanatory variables. RDA was calculated using the *vegan* library written by J. Oksanen (Finland) in the R language (Team 2004) and tested using 1000 permutations. We computed the R^2 of the RDA as the fraction of the total variation of the response matrix accounted for by the explanatory data table, and corrected it using the adjusted R^2 formula (Zar 1984):

$$\text{Adjusted } R^2 = 1 - [(1-R^2)\times((n-1)/(n-m-1))] \qquad (1)$$

where n is the sample size and m is the number of independent explanatory variables.

RESULTS

Species biological and behavioral traits were associated with different environmental variables across the four spatial scales in the two studied lakes. Results from the global R^2 statistic showed that the total variability of the species traits explained by the environment displayed the same pattern across spatial scales in Lac Drouin and Lac Paré (Figure 3.3). In the two lakes, the environmental variables explained a lower proportion of the species traits at fine (average adjusted $R^2 = -0.06$) and meso spatial scales (average adjusted $R^2 = 0.04$) than at broad (average adjusted $R^2 = 0.13$) and very broad scales (average adjusted $R^2 = 0.14$). Results from the global tests of significance, for Lac pare and Lac Drouin, showed that only the very broad and broad spatial scales displayed overall significant coefficients of determination.

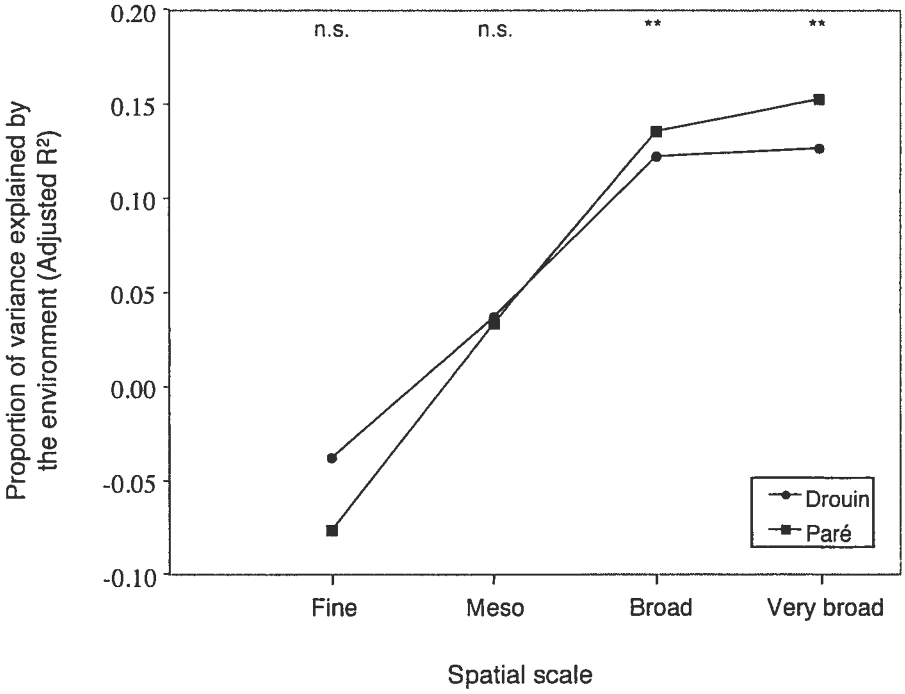


Figure 3.3 Proportion of the total variance of the species traits explained by the environmental variables at the four spatial scales in Lac Drouin (circles) and Lac Paré (squares).

Therefore, only the relationships at these two spatial scales are further described. For simplicity needs, we present a summary of the fourth-corner results found in matrix D. Complete results can be found in Electronic Appendix A.

Associations of species traits

Results from the PCA showed the presence of three groups composed of similar behavioral and morphological traits in Lac Drouin at very broad (Figure 3.4A) and broad spatial scales (Figure 3.4B).

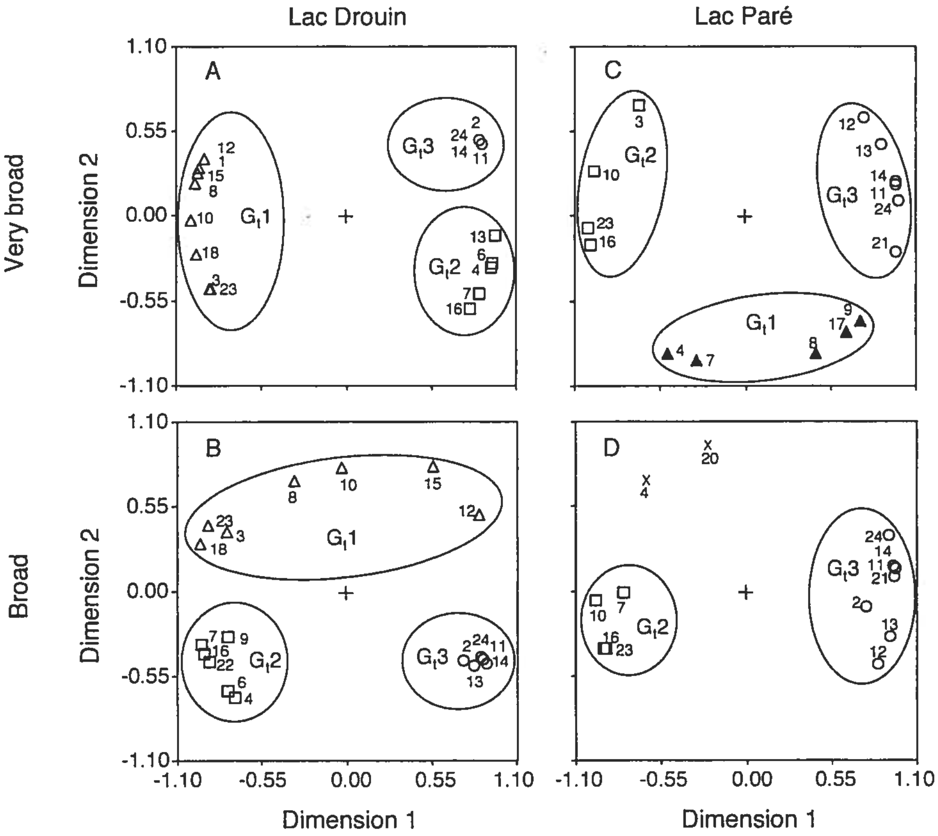


Figure 3.4 PCA ordinations showing the groups of species traits (G_t) for (A) Lac Drouin at very broad spatial scale, (B) Lac Drouin at broad spatial scale, (C) Lac Paré at very broad spatial scale, and (D) Lac Paré at broad spatial scale. Codes for the functional groups are found in Table 2. PCA were done using species traits that were significantly correlated to the environment, therefore the numbers indicating the species traits may vary among the four figures.

The first group of species traits (G_t1) included diurnal species feeding mainly on plants and supplemented its diet with zooplankton at the surface of water, and having a compressed body and a superior mouth position. This group was composed of small and large *N. crysoleucas* (Table 3.4; Δ). The second group of species traits (G_t2) was associated with insect larvae as the type of diet, feeding in the benthos and in mid-water, displaying a terminal mouth, and a fusiform body shape (at the broad spatial scale). Small and large *F. diaphanus*, small and large *L. gibbosus*, small and large *P. flavescens*, and small and large *S. atromaculatus* were the species composing that second group (Table 3.4; □). The third group (G_t3) included species traits such as zoobenthos as the types of diet, cylindrical body, and inferior position of the mouth. Members of that third group of species traits were small and large *C. commersoni* and small and large *A. nebulosus* (Table 3.4; O).

PCA on the traits-environment matrices displayed three groups at very broad scale (Figure 3.4C) and two groups at broad scale (Figure 3.4D) in Lac Paré. Since there was no species with superior mouth, the first group of species traits in Lac Paré differed slightly from the first group in Lac Drouin. That group (G_t1^*) was only present at very broad spatial scale and included species foraging on insect as the type of diet, the mid-water and water surface as feeding levels, and fusiform body shape. Two species composed this group, small and large *C. plumbeus* and small and large *S. atromaculatus* (Table 3.4; ▲). The second group of species traits (G_t2), present at the two spatial scales, included species with compressed body morphology, terminal position of the mouth, and diurnally active species. This group was composed of small and large *L. gibbosus* and small and large *P. flavescens* (Table 3.4; □).

Table 3.4 Classification of the fish species pertaining to each functional group in Lac Drouin and Lac Paré, obtained by PCA on the species behavioral and morphological trait matrices (i.e. matrix **B**). Δ : G_s1, ▲: G_s1*, □ : G_s2, O: G_s3.

	Functional group of species (G_s)	
Species	Lac Drouin	Lac Paré
A. nebulosus – small	O	O
A. nebulosus – large	O	
C. commersoni – small	O	O
C. commersoni – large	O	O
C. plumbeus – small		▲
C. plumbeus – large		▲
F. diaphanus – small	□	
F. diaphanus – large	□	
L. gibbosus – small	□	□
L. gibbosus – large	□	□
N. crysoleucas –small	Δ	
N. crysoleucas – large	Δ	
P. flavescens – small	□	□
P. flavescens – large	□	□
S. atromaculatus – small	□	▲
S. atromaculatus – large	□	▲

The third group of species traits (G_t3) was also present at the two spatial scales and included cylindrical body morphology, seasonal and daily migrating species with inferior mouth position, and nocturnally active. At the broad spatial scale

(Figure 3.4C), G_t3 also included the zoobenthos as the types of diet. This third group was represented by the small and large *C. commersoni* and small *A. nebulosus* (Table 3.4; O).

Species traits and environmental variables

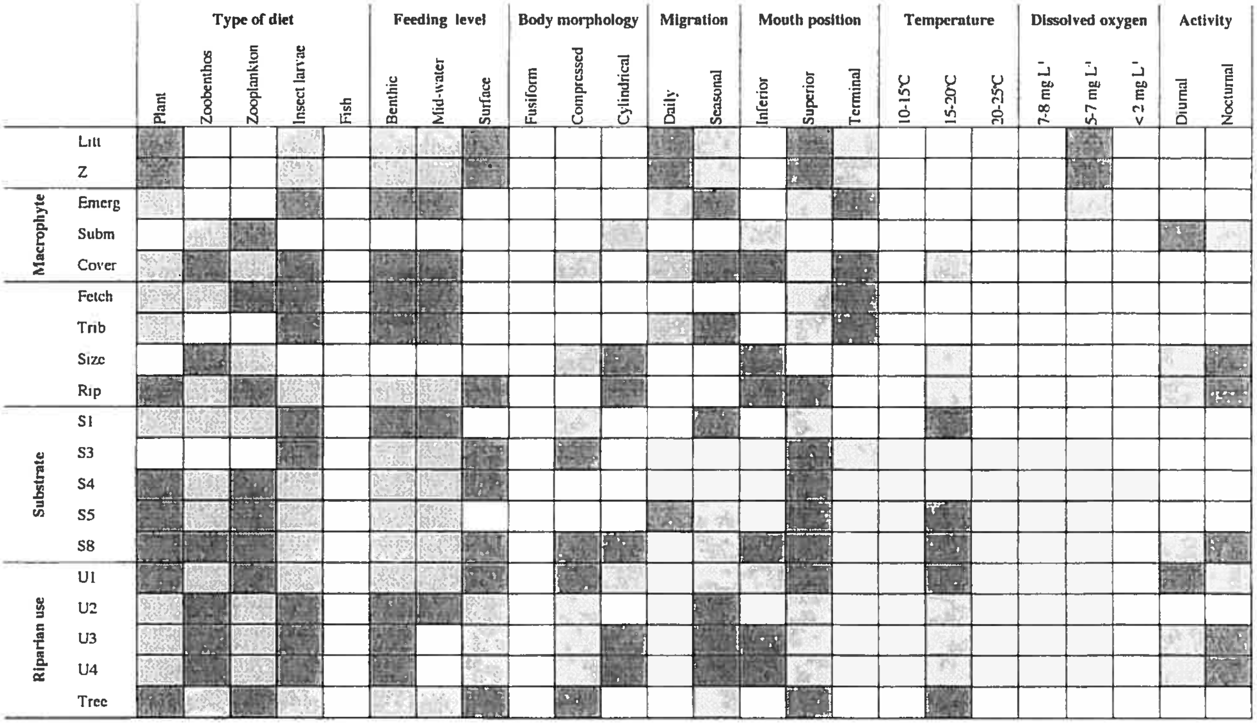
The correlations between species traits and environmental variables (matrix **D**) displayed mean values ranging from 0.082 to 0.145 in the two studied lakes (Table 3.5). The groups of species traits showed similar correlation values across spatial scales in Lac Drouin (two-way ANOVA with factors Groups and Scales, $F_{2,334}$ = 2.655, P = 0.072) and lac Paré (two-way ANOVA with the same factors, $F_{1,136}$ = 0.085, P = 0.771). However, correlation values in Lac Drouin were lower than in Lac Paré (one-way ANOVA, $F_{1,479}$ = 280.794, P < 0.001).

Table 3.5 Summary of the correlation values between the three groups (G_t) of species traits and the environment in the two lakes at very broad and broad spatial scales. Average values are in bracket.

	Group	Lac Drouin	Lac Paré
Very broad	G_t1	0.057 – 0.155 (0.090)	0.102 – 0.197 (0.145)
	G_t2	0.046 – 0.152 (0.091)	0.100 – 0.146 (0.123)
	G_t3	0.054 – 0.100 (0.082)	0.101 – 0.146 (0.120)
Broad	G_t1*	0.064 – 0.142 (0.093)	
	G_t2	0.066 – 0.117 (0.090)	0.101 – 0.147 (0.125)
	G_t3	0.057 – 0.145 (0.096)	0.093 – 0.147 (0.119)

Very broad scale.— Several correlations between the species traits and the environmental variables were significant at very broad scale in Lac Drouin (Figure

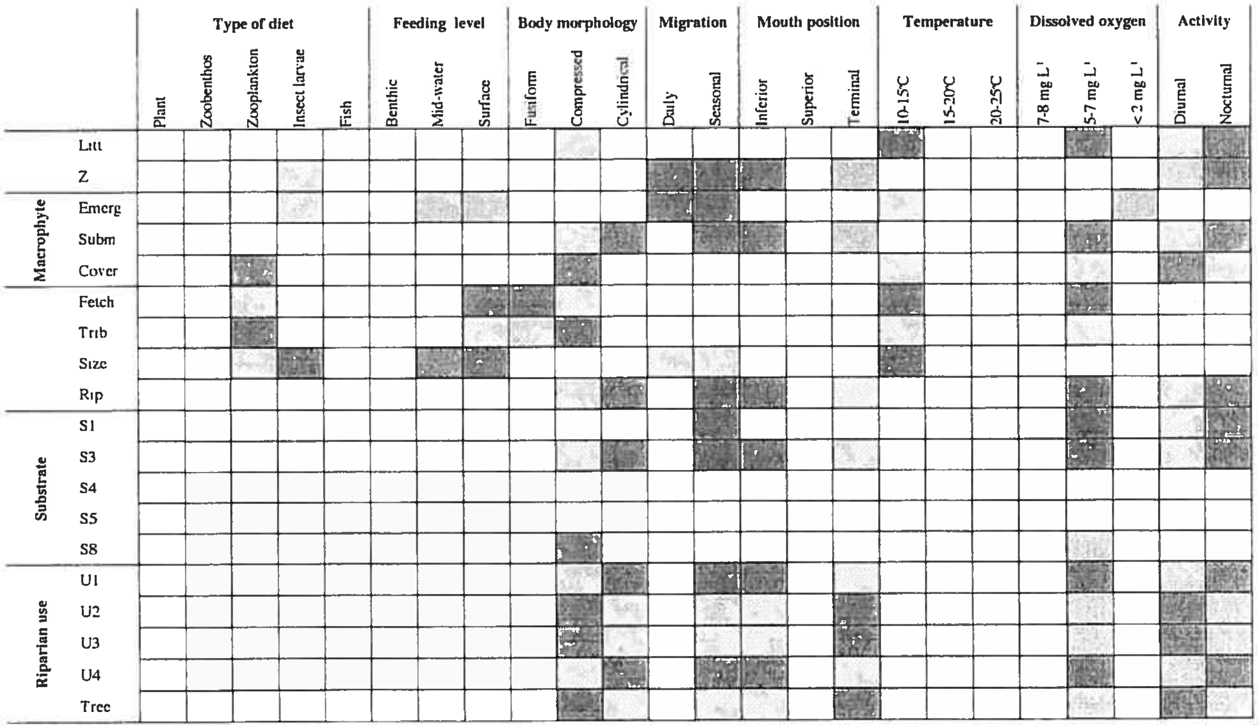
3.5). The surface group of species traits (G_t1) was correlated positively with the geomorphological variables (e.g. littoral slope: + and average depth: +) and a variety of substrates ranging from rocks (+) to woody debris (+). This group was negatively associated with emergent macrophytes and fetch. The mid-water group of species traits (G_t2) displayed trait-environment relationships opposite to those displayed by the G_t1 group. Hence, G_t2 was associated negatively with littoral slope and average depth and positively with emergent macrophytes, fetch and riparian uses (forest, beach, and bushes). The benthic group (G_t3) was associated with submersed macrophytes (–), bottom cover (+), surface area of the sampling site (+), sandy substrate (+), and different riparian uses (cabins: –, beaches: +, bushes: +).



		Type of diet					Feeding level			Body morphology			Migration		Mouth position			Temperature			Dissolved oxygen			Activity	
		Plant	Zoobenthos	Zooplankton	Insect larvae	Fish	Benthic	Mid-water	Surface	Fusiform	Compressed	Cylindrical	Daily	Seasonal	Inferior	Superior	Terminal	10-15°C	15-20°C	20-25°C	7-8 mg L⁻¹	5-7 mg L⁻¹	< 2 mg L⁻¹	Diurnal	Nocturnal
	Litt	■			▨		▨	▨	■				■	▨		■	▨					■			
	Z	■			▨		▨	▨	■				■	▨		■	▨					■			
Macrophyte	Emerg	▨			■		■	■					▨	■		▨	■					▨			
	Subm		▨	■								▨			▨									■	▨
	Cover	▨	■	▨	■		■	■			▨		▨	■	■	▨	■		▨						
	Fetch	▨	▨	■	■		■	■								▨	■								
	Trib	▨			■		■	■					▨	■		▨	■								
	Size		■	▨							▨	■			■				▨					▨	■
	Rip	■	▨	■	▨		▨	▨	■			■			■	■			▨					▨	■
Substrate	S1	▨	▨	▨	■		■	■			▨			■		▨			■						
	S3				■		▨	▨	■		■					■	▨								
	S4	■	▨	■	▨		▨	▨	■							■									
	S5	■	▨	■	▨		▨	▨					■	▨		■			■						
	S8	■	■	■	▨		▨	▨	■		■	■		▨	■	■			■					▨	■
Riparian use	U1	■	▨	■	▨		▨	▨	■		■	▨		▨	▨	■			■					■	▨
	U2	▨	■	▨	■		■	■	▨		▨			■		▨			▨						
	U3	▨	■	▨	■		■		▨		▨	■		■	■	▨			▨					▨	■
	U4	▨	■	▨	■		■		▨		▨	■		■	■	▨			▨					▨	■
	Tree	■	▨	■	▨		▨	▨	■		■			▨		■			■						

Figure 3.5 Correlations between species traits and environmental variables at very broad spatial scale in Lac Drouin. Significant positive correlations are in dark grey, significant negative correlations in light grey, and non-significant correlations in white. Codes for the environmental variables are found in Table 2.

The significant correlations between the groups of species traits and the environmental variables in Lac Paré were similar to those in Lac Drouin at very broad scale (Figure 3.6). As in Lac Drouin, the three groups displayed correlations mainly with depth and macrophytes. The surface group of species traits ($\mathrm{G_t1}$) was correlated negatively with average depth and emergent macrophytes but was associated positively with the surface area of the sampling site. The mid-water group of species traits ($\mathrm{G_t2}$) displayed similar trait-environment relationships as the first group, i.e. negative correlations with average depth and macrophytes. However, instead of emergent macrophytes as in $\mathrm{G_t1}$, the $\mathrm{G_t2}$ group was correlated with submersed macrophytes (–).

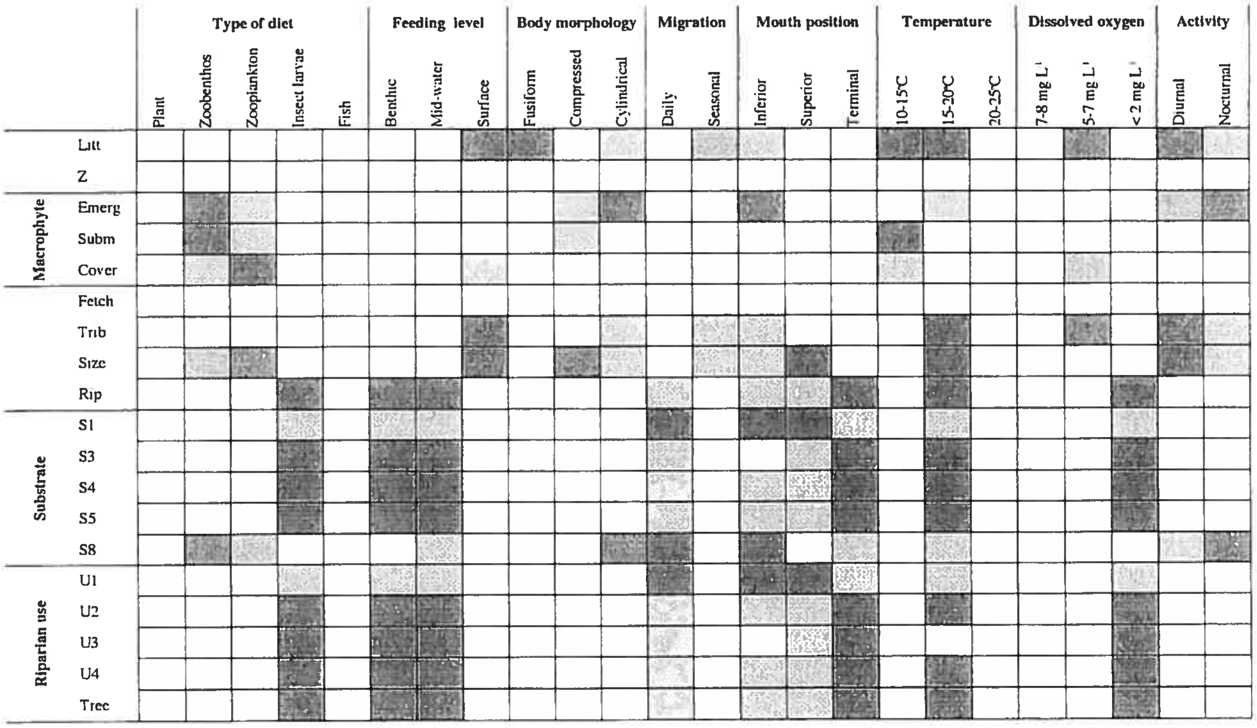


		Type of diet					Feeding level			Body morphology			Migration		Mouth position			Temperature			Dissolved oxygen			Activity	
		Plant	Zoobenthos	Zooplankton	Insect larvae	Fish	Benthic	Mid-water	Surface	Fusiform	Compressed	Cylindrical	Daily	Seasonal	Inferior	Superior	Terminal	10-15°C	15-20°C	20-25°C	7-8 mg L^{-1}	5-7 mg L^{-1}	< 2 mg L^{-1}	Diurnal	Nocturnal
	Litt										░							▓				▓		░	▓
	Z				░								▓	▓	▓		░							░	▓
Macrophyte	Emerg				░			░	░				▓	▓				░					░		
	Subm										░	▓		▓	▓		░					▓		░	▓
	Cover			▓							▓							░				░		▓	░
	Fetch			░					▓	▓	░							▓				▓			
	Trib			▓					░	░	▓							░				░			
	Size			░	▓			▓	▓				░	░				▓							
	Rip										░	▓		▓	▓		░					▓		░	▓
Substrate	S1													▓								▓		░	▓
	S3										░	▓		▓	▓		░					▓		░	▓
	S4																								
	S5																								
	S8										▓											░			
Riparian use	U1										░	▓		▓	▓		░					▓		░	▓
	U2										▓	░		░	░		▓					░		▓	░
	U3										▓	░		░	░		▓					░		▓	░
	U4										░	▓		▓	▓		░					▓		░	▓
	Tree										▓	░		░	░		▓					░		▓	░

Figure 3.6 Correlations between species traits and environmental variables at very broad spatial scale in Lac Paré. Significant positive correlations are in dark grey, significant negative correlations in light grey, and non-significant correlations in white. Codes for the environmental variables are found in Table 2.

In addition, G_t2 was also associated with rocks (–) and riparian trees (+). The benthic group of species traits (G_t3) displayed exactly the same correlations as the second group (G_t2), but the traits-environment correlations were of opposite signs. Therefore, G_t3 was correlated to the average depth (+), submersed macrophytes (–), rocks (+), and riparian trees (–).

Broad scale.— The significant correlations between the groups of species traits and the environmental variables were mostly related to substrate and riparian use at broad scale in Lac Drouin (Figure 3.7). The surface group of species (G_t1) displayed significant associations with the surface area of the sampling sites (+) and the presence of cabins on the shore (+).

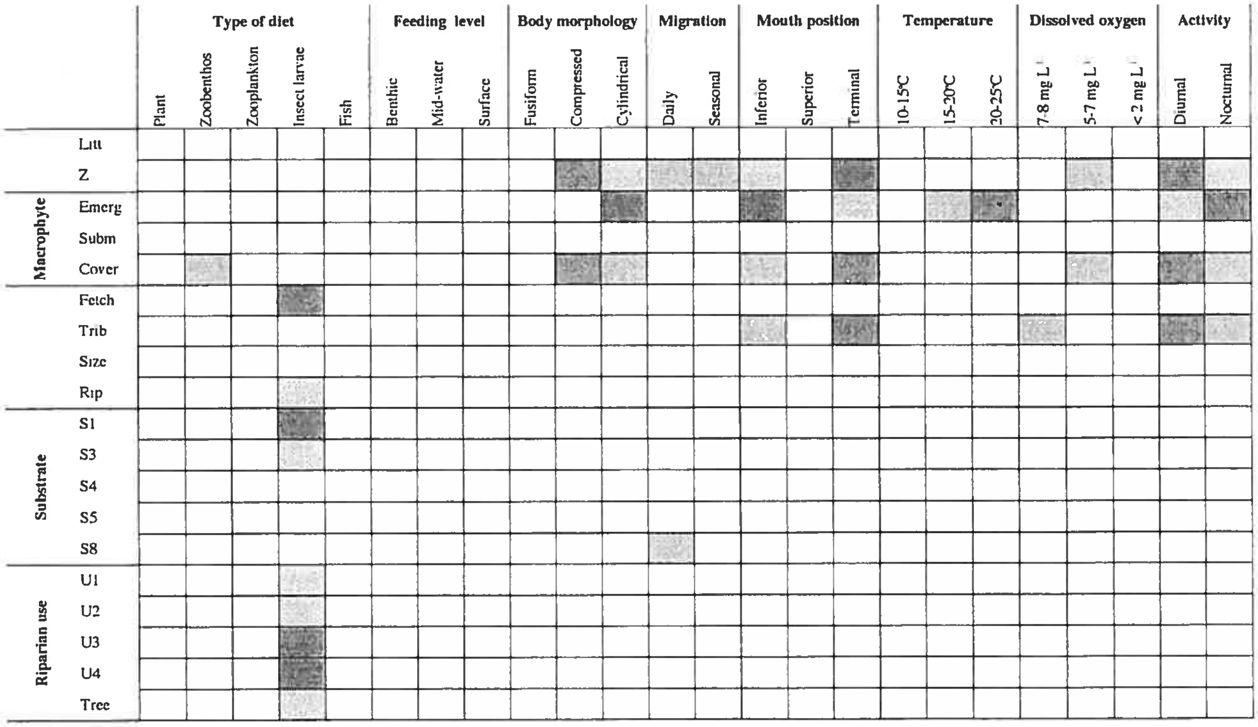


		Type of diet					Feeding level			Body morphology			Migration		Mouth position			Temperature			Dissolved oxygen			Activity	
		Plant	Zoobenthos	Zooplankton	Insect larvae	Fish	Benthic	Mid-water	Surface	Fusiform	Compressed	Cylindrical	Daily	Seasonal	Inferior	Superior	Terminal	10-15°C	15-20°C	20-25°C	7-8 mg L'	5-7 mg L'	< 2 mg L'	Diurnal	Nocturnal
	Litt								▓	▓		░		░	░			▓	▓			▓		▓	░
	Z																								
Macrophyte	Emerg		▓	░							░	▓			▓				░					░	▓
	Subm		▓	░							░							▓							
	Cover		░	▓					░									░				░			
	Fetch																								
	Trib								▓			░		░	░				▓			▓		▓	░
	Size		░	▓					▓		▓	░		░	░	▓			▓					▓	░
	Rip				▓		▓	▓					░		░	░	▓		▓				▓		
Substrate	S1				░		░	░					▓		▓	▓	░		░				░		
	S3				▓		▓	▓					░			░	▓		▓				▓		
	S4				▓		▓	▓					░		░	░	▓		▓				▓		
	S5				▓		▓	▓					░		░	░	▓		▓				▓		
	S8		▓	░				░				▓	▓		▓		░		░					░	▓
Riparian use	U1				░		░	░					▓		▓	▓	░		░				░		
	U2				▓		▓	▓					░		░	░	▓		▓				▓		
	U3				▓		▓	▓					░			░	▓						▓		
	U4				▓		▓	▓					░		░	░	▓		▓				▓		
	Tree				▓		▓	▓					░		░	░	▓		▓				▓		

Figure 3.7 Correlations between species traits and environmental variables at broad spatial scale in Lac Drouin. Significant positive correlations are in dark grey, significant negative correlations in light grey, and non-significant correlations in white. Codes for the environmental variables are found in Table 2.

This group of species traits was correlated negatively with all types of substrates except sand and woody debris. Species traits from the mid-water group (G_t2) showed an opposite correlation pattern compared to G1, as they displayed positive associations with all types of substrates except sand and woody debris. The benthic group of species traits (G_t3) was mostly associated to rocks (+) and emergent macrophytes (+). Negative correlations were found with boulders and rocks for G_t3.

Trait-environment relationships for the G_t2 were the same as for the G_t3 at the broad spatial scale in Lac Paré. However, the two groups of species traits displayed inverse trait-environment relationships (Figure 3.8). For instance, the mid-water group of species traits (G_t2) was associated to average depth (+), emergent macrophytes (–), bottom cover (+), and distance to the closest tributary (+).



		Type of diet					Feeding level			Body morphology			Migration		Mouth position			Temperature			Dissolved oxygen			Activity	
		Plant	Zoobenthos	Zooplankton	Insect larvae	Fish	Benthic	Mid-water	Surface	Fusiform	Compressed	Cylindrical	Daily	Seasonal	Inferior	Superior	Terminal	10-15°C	15-20°C	20-25°C	7-8 mg L⁻¹	5-7 mg L⁻¹	< 2 mg L⁻¹	Diurnal	Nocturnal
	Litt																								
	Z										▓	░	░	░	░		▓					░		▓	░
Macrophyte	Emerg											▓			▓		░		░	▓				░	▓
	Subm																								
	Cover		░								▓	░			░		▓					░		▓	░
	Fetch				▓																				
	Trib														░		▓				░			▓	░
	Size																								
	Rip				░																				
Substrate	S1				▓																				
	S3				░																				
	S4																								
	S5																								
	S8												░												
Riparian use	U1				░																				
	U2				░																				
	U3				▓																				
	U4				▓																				
	Tree				░																				

Figure 3.8 Correlations between species traits and environmental variables at broad spatial scale in Lac Paré. Significant positive correlations are in dark grey, significant negative correlations in light grey, and non significant correlations in white. Codes for the environmental variables are found in Table 2.

The benthic group (G_t3) was associated negatively to average depth, bottom cover, and distance to the closest tributary but was correlated positively to emergent macrophytes. The type of diet (insect larvae) was not correlated with other species traits but showed significant associations with substrates (sand and rock) and riparian uses.

DISCUSSION

Our study aimed to assess the presence of ecomorphological relationships in the organization of two littoral fish communities located on the Canadian Shield. While the results showed multiple correlations between the species traits (morphological and behavioral) and habitat characteristics, associations among specific species traits, suggested the presence of three functional groups of species. The species traits within a same functional group varied similarly with habitat conditions across spatial scales, confirming the presence of spatially structured ecomorphological relationships in the two studied lakes.

Functional feeding groups

Associations among the species biological traits that are concordant across spatial scales suggest that the spatial variations in the abundance of a species may be linked to its trophic level and morphological traits (Tscharntke and Brandl 2004). Fish species in the two studied lakes were segregated by their vertical positions in the water column (Werner et al. 1977). Three functional feeding groups (sensu Gatz 1979b) were distinguished according to the position of the mouth, body morphology, the type of diet, and the feeding level at which they foraged: superior-surface (G_t1), terminal-mid-water (G_t2), and inferior-benthic (G_t3). These results support early studies stating that the position of the mouth would either be an indicator of the location of the prey relative to the fish or of the depth within the water column at which a fish will obtain its food, given the fact that particular prey are mostly abundant in particular layers of the water column (Schutz and Northcote 1972, Gatz 1979b). Concurrently with the position of the mouth, the morphology of the body occupies an important place in the feeding performance of fish species (Hjelm et al. 2003). We observed that the surface-feeding group was associated with compressed body, whereas the mid-water-feeding group displayed fusiform body shape, and the benthic feeders displayed cylindrical body shape. Cylindrical shape with inferior mouth would optimize benthivory (Hjelm et al. 2003) as opposed to fusiform body shape with terminal mouth which would optimize zooplanktivory (Norton 1995). Hence large benthic fish would meet their energetic needs by foraging on prey that maximize the perdator's energy gains (Werner and Gilliam 1984).

Comparison between the two studied lakes showed that the littoral fish communities of Lac Paré and Lac Drouin shared five of their eight species (63%). *N. crysoleucas* and *F. diaphanus* were, however, absent from Lac Paré, whereas the lake chub *C. plumbeus*, was present in Lac Paré but absent in Lac Drouin. Despite these differences in species composition, the two lakes showed similar ecomorphological relationships among their fish communities, notably at the very broad spatial scale. This brings support to the hypothesis that members of a same functional feeding group tend to have similar morphologies and some degree of diet specialization (Angermeier and Winston 1998).

Multiscale habitat use

Ecological inference from the species traits and the environmental variables suggested the importance of the structural complexity of the habitat in the organization of fish communities (Crowder and Cooper 1982, Eklöv 1997, Weaver et al. 1997, Grenouillet and Pont 2001). This influence was observed on two levels: within and between spatial scale. The low values displayed by the correlation coefficients limit, however, our interpretation of these functional habitat uses. Correlation values, although significant, reached 20% in the best case. This could be explained notably by the 'indirect' nature of the information gathered for the fish species traits. Several studies observed that, beyond ontogenetic shift, fish species could display variable morphologies according to abiotic factors and/or biotic interactions along the temporal scale (Taylor 1999). By using general characteristics of the fish species from the literature and associating them with specific observations (in place and time), we may have generalized our results and thereby weakened our traits-environment relationships.

Within-scale complexity.— In Lac Drouin, at very broad spatial scale, water depth and macrophytes were important factors in habitat segregation among the littoral fish species (Beauchamp et al. 1994, Weaver et al. 1997, Grenouillet and Pont 2001). As the environmental conditions shifted from areas of low structural complexity such as deep sites with low abundance of emergent macrophytes to shallow areas with high density of emergent macrophytes, the fish assemblages near the surface shifted from surface feeders (G_t1) to mid-water feeders (G_t2). The benthic feeders (G_t3) were associated to large areas of dense bottom cover (i.e. carpet of *M. spicatum*) and sandy substrate. Several studies showed that the diversity and abundance of invertebrate food associated with nearshore macrophytes allow the coexistence of multiple species dietary specializations (Werner et al. 1977, Grenouillet and Pont 2001). The abundance of microcrustaceans varies widely among emergent and submersed macrophytes as well as between habitat depths (Paterson 1993). Cladoceran species, composing the food basis of many surface-feeding fish (G_s1) (e.g. *N. crysoleucas*; Keast and Webb 1966), predominate in deep sites (Paterson 1993). Insect larvae (odonata and chironomids), which are the preferred prey of the mid-water group (G_s2), are usually very abundant in shallow sites with high densities of emergent macrophytes (James et al. 1998, Weatherhead and James 2001). Although prey items (plankton and invertebrates), in either the water layers or the stomach contents of the species, have not been sampled/counted in our study, our results agree with other studies (Grenouillet and Pont 2001, Thompson et al. 2001) that the prey distribution among habitats represents an important factor in the spatial segregation of fish species.

Differences in the relationships between the biological traits and the environment displayed by the mid-water group (G_t2) and the benthic group (G_t3) were observed in the two lakes. In Lac Drouin, the two groups used different habitats whereas they used the same habitat in Lac Paré. This situation could be explained by the species composition of the mid-water group (G_s2) in Lac Paré. In that lake, the G_s2 group was exclusively composed of *L. gibbosus* and *P. flavescens*, whereas in Lac Drouin the G_s2 group was composed of four species including these two. However, *L. gibbosus* and *P. flavescens* are species displaying physiological attributes allowing benthic behavior. Hence, *L. gibbosus* has heavy, molariform pharyngeal teeth enabling it to crush the hard shells of gastropods, which may represent up to 90% of its diet in some lakes (Werner et al. 1977). *P. flavescens* with its sub-terminal mouth, is known to switch from zooplanktivory to benthivory as it increases in size (Post and McQueen 1988). Therefore, the presence of these two species only in group G_t2 of Lac Paré may explain the utilization of the same habitat as G_t3, the benthic group.

Among-scale complexity.— Since habitat complexity increases the number of potential niches, thereby providing refuge for more fish species, the number of functional groups would be expected to increase with habitat complexity (Figure 3.9). Our study supports this complexity assumption, as the three functional groups at very broad spatial scale were separated, in both lakes, by several environmental variables including average depths, different macrophytes densities (emergent, submersed and bottom cover), and rocky and woody substrates. At broad spatial scale (patches representing 10–20% of the total perimeter of our lakes), fish species was partitioned along a smaller number of habitat variables representing less complex structures. As the number of potential habitats decreases, fewer feeding strategies and specialized species are expected. Consequently, the presence of a restricted number of functional groups at that spatial scale was also expected. This situation was observed in Lac Paré in which the group represented by the surface feeders did not display significant correlations at broad spatial scale.

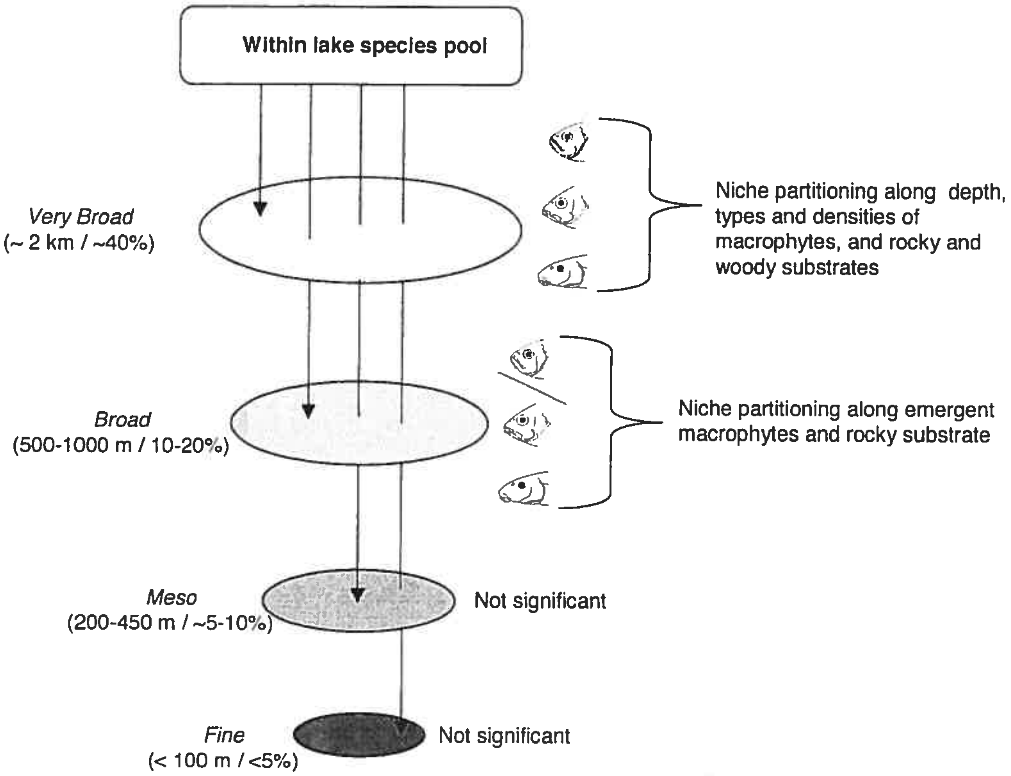


Figure 3.9 Schematic model of the spatial distribution of littoral fish species from Lac Drouin according to their biological and behavioral traits, across four spatial scales symbolized by the circle surface areas. The fish heads represent the three functional groups of species. The lengths refer to the shore lengths and the percentages are the portions of the perimeter of the lake covered by a habitat patch at the given scale.

Implications in fish-habitat modeling

Although the influence of the environmental variables changed according to the spatial scale, a high degree of persistence in the associations of species traits, forming the functional species groups, was observed across the spatial scales. For instance, 94% (Lac Drouin) and 90% (Lac Paré) of the species traits were classified in the same functional groups (G_t) at the very broad and the broad spatial scales. This result suggests that classification of the littoral fish species in functional units located above the species level would likely represent appropriate units of observation when studying littoral fish communities. From a management perspective, our conclusion is very appealing because it suggests to develop of habitat models based on functional groups (i.e. groups of species) instead of developing multiple habitat models for each of the member of the fish community (individual species).

Concurrently, since species trait-habitat relationships were significant at broader spatial scales, it appears that a threshold corresponding to 10-20% of the total perimeter of a lake would represent an appropriate sampling strategy when conducting within-lakes studies addressing fish community topics. It is likely at that threshold that the sampling of the littoral zone of lakes encompasses a sufficiently representative sample of the fish populations and of their associated physical habitat gradients.

Conclusion

A recent study done by Brind'Amour et al. (2005) showed that fish communities displayed several species responses to the spatially-structured littoral zone. They suggested that the scale-dependent segregation of species in different habitats might be related to their ecological range of specialization. In the present study, we build up on the work of Brind'Amour et al. (2005) but suggested that functional relationships between fish species and their habitat are principally established on the criteria of where and how resources are used by species within the water column. By considering multiple spatial scales, we emphasized the influence of the interaction between the spatial and the environmental (i.e. habitat characteristics) components on the functional organization of littoral fish communities. This conclusion is in agreement with Brind'Amour and Boisclair (submitted) who recently observed that habitat patches of varying sizes in the littoral zones of a lake were playing an important role as functional units for fish species and fish of different size classes. The development of fish habitat models including variables referring to the spatial and ecological components of habitats (e.g. spatial arrangement) contributed to explain higher proportion of fish-habitat relationships likely because it included functional information on different habitat requirements of fish species.

Given the increasing threat of loss of biodiversity in lake ecosystems, it is a necessity to understand the ecological mechanisms influencing the conservation of species diversity in littoral fish communities. Our study represents a contribution to the detection, on quantitative and statistical bases, of the potential mechanisms explaining the scale-dependent influence of environmental complexity on the community organization and species interaction of littoral fish in lakes.

WEB APPENDIX A

Table A.1 Correlations from the fourth-corner analysis between species traits and environmental variables at the very broad spatial scale in Lac Drouin. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Litt	0.133	-0.011	0.014	-0.129	0.009	-0.107	-0.149	0.105	-0.053	0.058	-0.013	0.086	-0.084	-0.013	0.155	-0.129	-0.012	0.040	-0.039	0.044	0.060	-0.005
P	0.002	0.706	0.678	0.002	0.808	0.006	0.002	0.002	0.090	0.090	0.350	0.014	0.016	0.350	0.003	0.003	0.790	0.200	0.200	0.148	0.036	0.762
Z	0.130	-0.025	0.027	-0.126	0.002	-0.105	-0.141	0.104	-0.051	0.062	-0.023	0.084	-0.083	-0.023	0.152	-0.121	-0.021	0.046	-0.035	0.040	0.059	-0.003
P	0.002	0.488	0.436	0.002	0.966	0.006	0.002	0.002	0.108	0.057	0.240	0.016	0.010	0.240	0.003	0.004	0.606	0.142	0.240	0.172	0.036	0.846
Emerg	-0.121	0.044	-0.048	0.118	0.010	0.099	0.125	-0.099	0.047	-0.066	0.038	-0.078	0.080	0.038	-0.144	0.104	0.034	-0.054	0.029	-0.033	-0.056	-0.002
P	0.002	0.188	0.166	0.004	0.770	0.010	0.002	0.002	0.136	0.051	0.136	0.026	0.008	0.120	0.003	0.008	0.418	0.088	0.336	0.286	0.046	1.000
Subm	0.035	-0.100	0.105	-0.037	-0.051	-0.036	-0.012	0.038	-0.010	0.052	-0.078	0.024	-0.034	-0.078	0.051	0.003	-0.069	0.063	0.006	-0.007	0.020	0.017
P	0.250	0.004	0.002	0.280	0.148	0.310	0.692	0.206	0.370	0.070	0.024	0.482	0.286	0.024	0.164	0.492	0.060	0.060	0.880	0.830	0.480	0.614
Cover	-0.102	0.066	-0.070	0.101	0.024	0.087	0.098	-0.087	0.038	-0.067	0.054	-0.067	0.071	0.054	-0.125	0.077	0.048	-0.062	0.020	-0.023	-0.048	-0.007
P	0.002	0.050	0.044	0.014	0.484	0.020	0.008	0.010	0.110	0.042	0.088	0.048	0.018	0.044	0.006	0.036	0.242	0.050	0.480	0.452	0.092	0.866
Fetch	-0.104	-0.067	0.068	0.098	-0.049	0.076	0.137	-0.073	0.045	-0.016	-0.048	-0.065	0.056	-0.048	-0.113	0.129	-0.043	0.010	0.043	-0.048	-0.043	0.019
P	0.002	0.036	0.044	0.006	0.156	0.028	0.002	0.012	0.243	0.290	0.243	0.052	0.090	0.087	0.004	0.003	0.232	0.784	0.150	0.114	0.128	0.448
Tribut	-0.122	-0.045	0.044	0.117	-0.039	0.093	0.152	-0.090	0.051	-0.033	-0.030	-0.078	0.070	-0.030	-0.136	0.139	-0.027	-0.007	0.045	-0.050	-0.052	0.015
P	0.002	0.210	0.214	0.004	0.262	0.006	0.002	0.004	0.126	0.288	0.288	0.018	0.046	0.205	0.003	0.003	0.426	0.810	0.126	0.108	0.060	0.564
Size	-0.052	0.096	-0.100	0.053	0.046	0.050	0.033	-0.051	0.017	-0.057	0.075	-0.035	0.044	0.075	-0.070	0.016	0.066	-0.065	0.000	0.000	-0.027	-0.016
P	0.094	0.006	0.002	0.146	0.196	0.168	0.306	0.086	0.289	0.050	0.030	0.310	0.168	0.030	0.068	0.333	0.074	0.042	1.000	1.000	0.328	0.658
Rip	-0.089	0.087	-0.090	0.086	0.036	0.075	0.073	-0.083	0.029	-0.068	0.074	-0.055	0.071	0.074	-0.111	0.053	0.057	-0.073	0.014	-0.016	-0.045	-0.012
P	0.006	0.010	0.010	0.020	0.298	0.034	0.042	0.010	0.165	0.033	0.033	0.114	0.022	0.026	0.009	0.064	0.162	0.014	0.638	0.602	0.110	0.742
S1	0.086	-0.077	0.081	-0.085	-0.032	-0.075	-0.078	0.073	-0.033	0.064	-0.060	0.057	-0.061	-0.060	0.107	-0.058	-0.056	0.061	-0.012	0.014	0.041	0.010
P	0.010	0.020	0.014	0.022	0.362	0.042	0.034	0.016	0.143	0.048	0.064	0.094	0.046	0.064	0.012	0.064	0.160	0.048	0.664	0.638	0.148	0.796
S3	0.042	0.007	0.010	-0.086	-0.006	-0.087	-0.087	0.033	-0.026	0.020	0.010	0.092	0.032	0.010	0.082	-0.078	-0.001	-0.009	-0.029	0.034	0.050	-0.045
P	0.140	0.842	0.762	0.024	0.868	0.018	0.012	0.264	0.648	0.648	0.648	0.016	0.294	0.387	0.038	0.027	1.000	0.790	0.318	0.258	0.066	0.136
S4	0.084	-0.071	0.076	-0.085	-0.030	-0.075	-0.079	0.069	-0.034	0.062	-0.054	0.058	-0.056	-0.054	0.105	-0.060	-0.055	0.056	-0.012	0.014	0.039	0.009
P	0.012	0.036	0.020	0.022	0.396	0.050	0.032	0.022	0.140	0.054	0.090	0.090	0.068	0.090	0.018	0.090	0.168	0.076	0.674	0.646	0.162	0.826
S5	0.086	-0.078	0.082	-0.085	-0.032	-0.075	-0.077	0.074	-0.032	0.064	-0.061	0.057	-0.061	-0.061	0.107	-0.057	-0.057	0.062	-0.012	0.014	0.041	0.010
P	0.010	0.020	0.014	0.022	0.360	0.040	0.034	0.014	0.144	0.048	0.060	0.094	0.044	0.060	0.012	0.060	0.158	0.046	0.664	0.634	0.146	0.790
S8	-0.091	0.096	-0.098	0.086	0.040	0.075	0.067	-0.093	0.024	-0.071	0.088	-0.051	0.081	0.088	-0.114	0.047	0.055	-0.086	0.015	-0.017	-0.049	-0.014
P	0.006	0.008	0.006	0.018	0.238	0.028	0.056	0.006	0.208	0.016	0.012	0.138	0.014	0.008	0.006	0.086	0.160	0.008	0.626	0.566	0.080	0.696
U1	0.089	-0.089	0.092	-0.086	-0.037	-0.075	-0.072	0.083	-0.030	0.069	-0.075	0.054	-0.072	-0.075	0.111	-0.053	-0.059	0.074	-0.013	0.015	0.044	0.013
P	0.006	0.010	0.008	0.020	0.292	0.034	0.044	0.010	0.156	0.024	0.024	0.118	0.020	0.024	0.009	0.066	0.140	0.014	0.644	0.614	0.118	0.718
U2	-0.087	0.081	-0.085	0.086	0.034	0.075	0.076	-0.077	0.031	-0.066	0.065	-0.056	0.064	0.065	-0.108	0.056	0.057	-0.066	0.013	-0.015	-0.042	-0.011
P	0.008	0.020	0.012	0.022	0.336	0.038	0.034	0.010	0.149	0.048	0.054	0.098	0.034	0.054	0.012	0.054	0.156	0.026	0.656	0.622	0.130	0.786
U3	-0.092	0.100	-0.101	0.085	0.042	0.075	0.064	-0.098	0.021	-0.072	0.095	-0.049	0.085	0.095	-0.115	0.044	0.054	-0.092	0.016	-0.018	-0.052	-0.015
P	0.006	0.006	0.004	0.020	0.212	0.026	0.072	0.002	0.235	0.012	0.009	0.174	0.008	0.006	0.003	0.103	0.170	0.004	0.604	0.538	0.070	0.676
U4	-0.092	0.100	-0.101	0.086	0.041	0.075	0.067	-0.093	0.025	-0.073	0.089	-0.051	0.082	0.089	-0.115	0.047	0.058	-0.087	0.015	-0.017	-0.048	-0.015
P	0.006	0.006	0.004	0.020	0.226	0.028	0.058	0.006	0.200	0.012	0.012	0.148	0.014	0.008	0.003	0.085	0.142	0.008	0.628	0.578	0.082	0.684
Tree	0.087	-0.080	0.084	-0.086	-0.033	-0.075	-0.076	0.077	-0.031	0.065	-0.064	0.057	-0.064	-0.064	0.108	-0.056	-0.056	0.065	-0.013	0.015	0.042	0.011
P	0.008	0.020	0.012	0.022	0.342	0.036	0.034	0.010	0.152	0.048	0.054	0.094	0.040	0.054	0.012	0.054	0.162	0.032	0.656	0.624	0.128	0.788

Table A.2 Correlations from the fourth-corner analysis between species traits and environmental variables at the broad spatial scale in Lac Drouin. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.034	-0.015	0.008	0.006	-0.022	0.014	0.033	0.141	0.083	-0.014	-0.118	-0.043	-0.109	-0.118	0.027	0.049	0.084	0.125	-0.020	0.030	0.082	0.020	0.118	-0.118
P	0.254	0.658	0.790	0.848	0.542	0.712	0.296	0.002	0.012	0.315	0.006	0.214	0.002	0.006	0.250	0.150	0.036	0.002	0.560	0.356	0.006	0.554	0.004	0.004
Z	0.054	-0.014	0.003	-0.044	-0.006	-0.056	-0.026	0.058	0.004	0.003	-0.012	0.040	-0.027	-0.012	0.063	-0.048	0.025	-0.003	-0.007	0.012	0.044	-0.007	0.012	-0.012
P	0.078	0.664	0.936	0.236	0.826	0.108	0.408	0.068	1.000	1.000	1.000	0.272	0.372	0.343	0.153	0.160	0.518	0.888	0.798	0.682	0.118	0.808	0.686	0.686
Emerg	-0.029	0.145	-0.142	0.018	0.060	0.016	-0.045	-0.048	0.009	-0.066	0.105	0.003	0.061	0.105	-0.039	-0.029	0.065	-0.103	0.005	-0.015	-0.015	-0.015	-0.105	0.105
P	0.362	0.002	0.002	0.670	0.078	0.634	0.174	0.136	0.389	0.044	0.003	0.956	0.072	0.003	0.302	0.302	0.086	0.002	0.842	0.614	0.622	0.648	0.002	0.002
Subm	0.012	0.111	-0.101	-0.007	0.055	-0.013	-0.026	0.020	0.054	-0.079	0.050	0.028	0.061	0.050	-0.010	-0.021	0.091	-0.057	0.003	-0.007	0.053	-0.021	-0.050	0.050
P	0.728	0.002	0.002	0.884	0.102	0.708	0.456	0.566	0.112	0.015	0.112	0.414	0.058	0.168	0.556	0.556	0.018	0.058	0.898	0.816	0.066	0.550	0.112	0.112
Cover	-0.054	-0.075	0.084	0.014	-0.047	0.012	0.022	-0.092	-0.070	0.057	0.018	-0.001	0.038	0.018	-0.027	0.013	-0.101	-0.008	0.004	0.002	-0.072	-0.009	-0.018	0.018
P	0.064	0.020	0.018	0.692	0.190	0.700	0.466	0.004	0.051	0.080	0.274	0.994	0.212	0.672	0.672	0.672	0.016	0.810	0.908	0.938	0.008	0.776	0.548	0.548
Fetch	0.044	-0.046	0.044	-0.014	0.010	-0.009	0.016	0.033	0.019	0.005	-0.044	0.006	-0.015	-0.044	0.017	0.011	-0.017	0.035	0.010	-0.016	0.024	0.018	0.044	-0.044
P	0.138	0.174	0.194	0.686	0.756	0.786	0.674	0.320	0.562	0.562	0.222	0.864	0.612	0.222	0.604	0.604	0.618	0.280	0.776	0.608	0.458	0.570	0.148	0.148
Tribut	0.051	-0.062	0.050	-0.039	-0.022	-0.034	0.007	0.130	0.040	0.031	-0.127	0.004	-0.100	-0.127	0.074	0.013	0.037	0.121	-0.035	0.041	0.076	-0.002	0.127	-0.127
P	0.086	0.054	0.116	0.278	0.494	0.316	0.788	0.002	0.202	0.202	0.003	0.890	0.002	0.003	0.052	0.358	0.322	0.002	0.262	0.208	0.014	0.896	0.002	0.002
Size	0.044	-0.135	0.127	-0.054	-0.063	-0.054	0.016	0.101	-0.002	0.076	-0.134	0.024	-0.088	-0.134	0.088	0.004	-0.025	0.127	-0.037	0.050	0.053	-0.012	0.134	-0.134
P	0.174	0.002	0.002	0.160	0.060	0.148	0.624	0.004	0.472	0.024	0.003	0.452	0.004	0.003	0.030	0.462	0.556	0.002	0.266	0.130	0.064	0.670	0.002	0.002
Rip	-0.014	-0.042	0.043	0.082	0.000	0.098	0.092	0.001	0.054	-0.021	-0.057	-0.097	-0.037	-0.057	-0.084	0.109	-0.024	0.071	0.044	-0.047	-0.019	0.071	0.057	-0.057
P	0.662	0.182	0.172	0.014	1.000	0.006	0.010	0.968	0.111	0.258	0.111	0.004	0.260	0.037	0.018	0.009	0.498	0.026	0.158	0.130	0.542	0.018	0.074	0.074
S1	0.012	0.047	-0.049	-0.076	0.003	-0.091	-0.089	-0.005	-0.051	0.016	0.061	0.091	0.038	0.061	0.077	-0.105	0.025	-0.074	-0.040	0.042	0.016	-0.066	-0.061	0.061
P	0.724	0.134	0.134	0.034	1.000	0.012	0.010	0.894	0.136	0.311	0.087	0.008	0.258	0.038	0.038	0.009	0.478	0.018	0.210	0.190	0.598	0.032	0.058	0.058
S3	-0.018	-0.034	0.035	0.092	0.003	0.108	0.095	-0.006	0.057	-0.027	-0.050	-0.106	-0.035	-0.050	-0.095	0.114	-0.024	0.064	0.050	-0.054	-0.025	0.077	0.050	-0.050
P	0.586	0.276	0.280	0.004	0.854	0.002	0.010	0.838	0.135	0.193	0.135	0.002	0.288	0.062	0.006	0.006	0.526	0.044	0.114	0.086	0.390	0.008	0.124	0.124
S4	-0.014	-0.043	0.044	0.082	-0.001	0.097	0.092	0.001	0.054	-0.020	-0.057	-0.096	-0.037	-0.057	-0.083	0.109	-0.024	0.071	0.043	-0.046	-0.019	0.070	0.057	-0.057
P	0.672	0.174	0.164	0.016	1.000	0.008	0.010	0.950	0.112	0.265	0.108	0.004	0.258	0.036	0.022	0.009	0.496	0.028	0.168	0.132	0.548	0.020	0.072	0.072
S5	-0.013	-0.046	0.048	0.078	-0.002	0.093	0.090	0.004	0.052	-0.017	-0.060	-0.092	-0.037	-0.060	-0.079	0.106	-0.025	0.073	0.041	-0.043	-0.016	0.067	0.060	-0.060
P	0.714	0.140	0.142	0.030	1.000	0.010	0.010	0.910	0.126	0.298	0.096	0.006	0.258	0.032	0.030	0.009	0.486	0.018	0.200	0.176	0.592	0.032	0.064	0.064
S8	0.003	0.068	-0.071	-0.050	0.014	-0.063	-0.074	-0.015	-0.037	-0.005	0.073	0.065	0.039	0.073	0.048	-0.086	0.034	-0.083	-0.025	0.025	0.006	-0.049	-0.073	0.073
P	0.944	0.038	0.034	0.174	0.712	0.052	0.022	0.674	0.290	0.427	0.039	0.050	0.250	0.026	0.105	0.021	0.328	0.012	0.412	0.436	0.828	0.122	0.026	0.026
U1	0.013	0.045	-0.046	-0.079	0.002	-0.095	-0.091	-0.003	-0.053	0.018	0.059	0.094	0.037	0.059	0.081	-0.107	0.024	-0.072	-0.042	0.044	0.017	-0.068	-0.059	0.059
P	0.692	0.146	0.150	0.024	1.000	0.010	0.010	0.924	0.116	0.279	0.102	0.004	0.258	0.034	0.026	0.009	0.496	0.022	0.190	0.170	0.576	0.026	0.068	0.068
U2	-0.013	-0.045	0.047	0.078	-0.002	0.094	0.090	0.004	0.052	-0.018	-0.059	-0.093	-0.037	-0.059	-0.079	0.106	-0.024	0.073	0.041	-0.043	-0.016	0.068	0.059	-0.059
P	0.708	0.144	0.148	0.024	1.000	0.010	0.010	0.910	0.124	0.285	0.099	0.004	0.258	0.033	0.030	0.009	0.492	0.018	0.196	0.174	0.594	0.030	0.066	0.066
U3	-0.021	-0.030	0.030	0.097	0.005	0.113	0.097	-0.011	0.058	-0.031	-0.045	-0.110	-0.034	-0.045	-0.101	0.117	-0.024	0.059	0.053	-0.058	-0.029	0.081	0.045	-0.045
P	0.538	0.350	0.346	0.004	0.812	0.002	0.010	0.732	0.132	0.160	0.158	0.002	0.300	0.079	0.006	0.003	0.518	0.058	0.092	0.058	0.304	0.004	0.158	0.158
U4	-0.014	-0.042	0.043	0.082	0.000	0.098	0.092	0.001	0.054	-0.021	-0.057	-0.097	-0.037	-0.057	-0.084	0.109	-0.024	0.071	0.043	-0.046	-0.019	0.070	0.057	-0.057
P	0.666	0.180	0.170	0.016	1.000	0.006	0.010	0.956	0.112	0.257	0.108	0.004	0.258	0.036	0.020	0.009	0.498	0.028	0.162	0.130	0.544	0.018	0.072	0.072
Tree	-0.012	-0.047	0.049	0.076	-0.003	0.091	0.089	0.005	0.051	-0.016	-0.061	-0.091	-0.038	-0.061	-0.077	0.105	-0.025	0.074	0.040	-0.042	-0.015	0.066	0.061	-0.061
P	0.726	0.132	0.134	0.034	1.000	0.012	0.010	0.890	0.136	0.311	0.087	0.008	0.256	0.038	0.038	0.009	0.480	0.018	0.214	0.190	0.602	0.032	0.058	0.058

Table A.3 Correlations from the fourth-corner analysis between species traits and environmental variables at the meso spatial scale in Lac Drouin. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.015	-0.011	0.001	-0.051	0.025	-0.054	-0.064	0.013	-0.050	0.059	-0.019	0.041	-0.029	-0.019	0.067	-0.047	-0.023	0.013	-0.037	0.039	-0.003	-0.033	0.019	-0.019
P	0.584	0.764	0.980	0.152	0.422	0.122	0.030	0.652	0.098	0.081	0.273	0.224	0.350	0.273	0.102	0.168	0.550	0.656	0.230	0.196	0.960	0.264	0.546	0.546
Z	0.096	0.010	-0.008	-0.070	0.001	-0.046	-0.074	0.080	0.000	-0.012	0.022	0.043	-0.037	0.022	0.074	-0.079	0.003	0.014	0.013	-0.010	0.060	0.037	-0.022	0.022
P	0.002	0.780	0.832	0.054	0.964	0.178	0.022	0.006	0.786	0.786	0.786	0.192	0.210	0.262	0.042	0.030	0.962	0.654	0.646	0.716	0.038	0.224	0.524	0.524
Emerg	0.059	0.071	-0.068	-0.025	0.057	-0.029	-0.039	0.018	0.013	-0.068	0.100	0.042	0.052	0.100	0.011	-0.071	0.040	-0.072	0.032	-0.017	0.046	0.014	-0.100	0.100
P	0.032	0.032	0.042	0.484	0.092	0.388	0.226	0.570	0.330	0.032	0.015	0.210	0.098	0.015	0.385	0.042	0.306	0.022	0.256	0.588	0.080	0.606	0.010	0.010
Subm	0.002	-0.008	0.015	-0.057	0.013	-0.065	-0.049	-0.017	-0.045	0.039	0.007	0.070	0.042	0.007	0.051	-0.049	-0.019	-0.018	-0.037	0.039	0.005	-0.060	-0.007	0.007
P	0.934	0.848	0.700	0.110	0.660	0.060	0.122	0.582	0.249	0.249	0.406	0.026	0.184	0.406	0.243	0.243	0.648	0.556	0.232	0.236	0.832	0.058	0.812	0.812
Cover	-0.027	-0.028	0.033	0.080	-0.002	0.072	0.040	-0.075	0.007	-0.016	0.017	-0.064	0.024	0.017	-0.089	0.068	-0.086	-0.025	0.080	-0.084	-0.062	0.077	-0.017	0.017
P	0.324	0.368	0.312	0.026	0.970	0.060	0.248	0.012	0.933	0.933	0.933	0.084	0.444	0.328	0.033	0.052	0.038	0.424	0.020	0.010	0.018	0.008	0.656	0.656
Fetch	-0.064	-0.035	0.037	0.011	-0.038	0.020	0.046	-0.032	-0.030	0.052	-0.042	-0.020	-0.015	-0.042	-0.012	0.036	0.004	0.045	-0.062	0.059	-0.040	-0.057	0.042	-0.042
P	0.034	0.292	0.274	0.724	0.252	0.526	0.174	0.294	0.188	0.138	0.188	0.554	0.640	0.282	0.365	0.304	0.876	0.140	0.038	0.040	0.148	0.046	0.188	0.188
Tribut	0.021	-0.041	0.046	-0.034	-0.015	-0.023	-0.066	-0.048	-0.087	0.064	0.035	0.024	-0.011	0.035	0.034	-0.052	-0.097	-0.017	0.002	-0.001	-0.054	0.010	-0.035	0.035
P	0.450	0.176	0.146	0.344	0.576	0.456	0.064	0.116	0.009	0.022	0.115	0.456	0.758	0.230	0.230	0.183	0.014	0.544	0.946	0.932	0.048	0.724	0.230	0.230
Size	-0.034	-0.032	0.026	0.099	0.001	0.104	0.060	-0.086	0.003	-0.012	0.017	-0.098	-0.006	0.017	-0.107	0.084	-0.094	-0.017	0.083	-0.094	-0.089	0.098	-0.017	0.017
P	0.220	0.312	0.388	0.008	0.994	0.006	0.052	0.010	0.933	0.933	0.933	0.012	0.900	0.311	0.006	0.012	0.016	0.576	0.010	0.002	0.006	0.002	0.622	0.622
Rip	-0.023	-0.004	-0.002	0.024	-0.007	0.035	0.032	0.027	0.007	0.025	-0.058	-0.049	-0.070	-0.058	-0.008	0.042	0.043	0.068	-0.045	0.047	-0.011	-0.020	0.058	-0.058
P	0.446	0.852	1.000	0.488	0.832	0.348	0.334	0.366	0.418	0.386	0.102	0.130	0.018	0.102	0.424	0.252	0.278	0.028	0.128	0.136	0.660	0.488	0.068	0.068
S1	-0.019	-0.004	-0.001	0.021	-0.006	0.032	0.028	0.027	0.005	0.026	-0.056	-0.046	-0.070	-0.056	-0.004	0.038	0.040	0.067	-0.045	0.047	-0.011	-0.019	0.056	-0.056
P	0.524	0.866	1.000	0.568	0.846	0.392	0.412	0.346	0.451	0.358	0.120	0.172	0.022	0.120	0.455	0.286	0.298	0.030	0.130	0.138	0.670	0.502	0.080	0.080
S3	-0.028	-0.003	-0.003	0.030	-0.007	0.039	0.038	0.026	0.012	0.023	-0.061	-0.054	-0.070	-0.061	-0.013	0.049	0.046	0.069	-0.045	0.047	-0.012	-0.020	0.061	-0.061
P	0.348	0.872	0.976	0.416	0.824	0.288	0.270	0.378	0.434	0.434	0.075	0.104	0.012	0.075	0.375	0.170	0.248	0.026	0.136	0.134	0.658	0.486	0.050	0.050
S4	0.013	0.004	0.001	-0.014	0.005	-0.027	-0.019	-0.028	0.001	-0.029	0.051	0.041	0.070	0.051	-0.002	-0.029	-0.035	-0.064	0.045	-0.047	0.010	0.018	-0.051	0.051
P	0.688	0.858	1.000	0.720	0.866	0.480	0.564	0.338	0.480	0.342	0.165	0.252	0.022	0.165	0.456	0.422	0.356	0.034	0.136	0.148	0.682	0.524	0.110	0.110
S5	0.017	0.004	0.001	-0.018	0.006	-0.030	-0.024	-0.027	-0.002	-0.027	0.054	0.044	0.070	0.054	0.001	-0.034	-0.038	-0.066	0.045	-0.047	0.011	0.019	-0.054	0.054
P	0.594	0.870	1.000	0.632	0.858	0.428	0.476	0.338	0.478	0.350	0.138	0.202	0.022	0.138	0.493	0.342	0.320	0.032	0.130	0.140	0.680	0.504	0.092	0.092
S8	0.008	0.004	0.001	-0.009	0.003	-0.023	-0.013	-0.028	0.005	-0.030	0.046	0.037	0.070	0.046	-0.007	-0.022	-0.033	-0.062	0.044	-0.046	0.010	0.017	-0.046	0.046
P	0.818	0.868	1.000	0.796	0.890	0.560	0.682	0.334	0.432	0.324	0.210	0.298	0.024	0.210	0.552	0.552	0.392	0.034	0.138	0.142	0.704	0.570	0.140	0.140
U1	0.018	0.004	0.001	-0.020	0.006	-0.031	-0.026	-0.027	-0.004	-0.027	0.055	0.046	0.070	0.055	0.003	-0.036	-0.039	-0.066	0.045	-0.047	0.011	0.019	-0.055	0.055
P	0.550	0.878	1.000	0.590	0.856	0.402	0.434	0.346	0.459	0.352	0.126	0.186	0.020	0.126	0.469	0.306	0.304	0.032	0.130	0.140	0.680	0.508	0.084	0.084
U2	0.018	0.004	0.001	-0.019	0.006	-0.031	-0.025	-0.027	-0.003	-0.027	0.054	0.045	0.070	0.054	0.002	-0.035	-0.039	-0.066	0.045	-0.047	0.011	0.019	-0.054	0.054
P	0.574	0.876	1.000	0.612	0.858	0.414	0.454	0.338	0.468	0.352	0.138	0.188	0.020	0.138	0.477	0.326	0.312	0.032	0.130	0.142	0.676	0.508	0.092	0.092
U3	0.012	0.004	0.001	-0.013	0.004	-0.026	-0.018	-0.028	0.001	-0.029	0.050	0.040	0.070	0.050	-0.003	-0.028	-0.035	-0.064	0.045	-0.047	0.010	0.018	-0.050	0.050
P	0.704	0.866	0.998	0.730	0.872	0.492	0.582	0.338	0.475	0.342	0.174	0.256	0.022	0.174	0.447	0.442	0.362	0.034	0.138	0.144	0.682	0.542	0.116	0.116
U4	-0.020	-0.004	-0.001	0.021	-0.006	0.032	0.028	0.027	0.005	0.026	-0.056	-0.047	-0.070	-0.056	-0.005	0.038	0.041	0.067	-0.045	0.047	-0.011	-0.019	0.056	-0.056
P	0.520	0.874	1.000	0.560	0.848	0.378	0.408	0.346	0.446	0.360	0.114	0.166	0.020	0.114	0.451	0.276	0.294	0.030	0.130	0.140	0.670	0.504	0.076	0.076
Tree	0.018	0.004	0.001	-0.019	0.006	-0.031	-0.026	-0.027	-0.003	-0.027	0.055	0.045	0.070	0.052	0.003	-0.036	-0.039	-0.066	0.045	-0.047	0.011	0.019	-0.052	0.055
P	0.566	0.876	1.000	0.600	0.858	0.414	0.448	0.338	0.466	0.352	0.135	0.188	0.020	0.135	0.473	0.320	0.310	0.032	0.130	0.142	0.674	0.514	0.090	0.090

Table A.4 Correlations from the fourth-corner analysis between species traits and environmental variables at the fine spatial scale in Lac Drouin. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.005	-0.006	0.004	-0.020	-0.001	-0.014	-0.024	0.008	-0.029	0.031	-0.005	0.008	-0.027	-0.005	0.028	-0.022	-0.004	0.018	-0.026	0.031	-0.007	-0.016	0.005	-0.005
P	0.960	0.960	0.940	0.400	0.800	0.740	0.520	0.800	0.380	0.360	0.420	0.760	0.380	0.660	0.660	0.660	0.920	0.500	0.340	0.380	0.800	0.580	0.840	0.840
Z	-0.023	0.000	0.004	-0.011	0.007	-0.025	0.009	-0.029	0.005	-0.016	0.020	0.041	0.078	0.020	-0.007	-0.006	-0.014	-0.038	0.012	-0.013	0.013	-0.021	-0.020	0.020
P	0.400	1.000	1.000	0.840	0.680	0.500	0.760	0.320	0.690	0.690	0.690	0.200	0.020	0.690	0.780	0.780	0.780	0.180	0.720	0.680	0.680	0.340	0.460	0.460
Emerg	0.090	0.006	-0.003	-0.049	-0.005	-0.045	-0.090	0.034	-0.033	0.002	0.054	0.035	-0.031	0.054	0.061	-0.087	-0.028	-0.032	0.029	-0.021	0.017	0.043	-0.054	0.054
P	0.020	0.760	0.740	0.240	0.960	0.180	0.020	0.200	0.280	0.560	0.090	0.300	0.380	0.060	0.070	0.030	0.460	0.220	0.260	0.480	0.640	0.160	0.060	0.060
Subm	0.004	-0.002	0.005	0.006	-0.038	-0.001	0.038	0.052	0.055	-0.033	-0.035	-0.004	-0.007	-0.035	0.000	0.022	0.059	0.022	-0.003	0.003	0.048	-0.004	0.035	-0.035
P	0.760	1.000	0.900	0.900	0.260	0.900	0.260	0.100	0.150	0.160	0.160	0.920	0.800	0.240	0.480	0.400	0.200	0.360	0.960	0.900	0.080	0.880	0.160	0.160
Cover	-0.023	0.000	-0.006	0.019	-0.020	0.005	0.004	-0.003	0.020	-0.022	0.006	-0.006	0.016	0.006	-0.018	0.013	-0.022	-0.018	0.044	-0.041	0.006	0.035	-0.006	0.006
P	0.540	1.000	0.760	0.720	0.600	1.000	0.980	0.980	0.930	0.930	0.930	0.980	0.620	1.000	1.000	1.000	0.460	0.480	0.180	0.280	0.880	0.280	0.840	0.840
Fetch	-0.083	-0.003	0.000	0.055	0.000	0.057	0.092	0.006	0.059	-0.005	-0.094	-0.055	-0.006	-0.094	-0.058	0.109	0.050	0.074	-0.034	0.025	0.003	-0.033	0.094	-0.094
P	0.020	0.820	1.000	0.160	0.900	0.080	0.020	0.840	0.060	0.530	0.030	0.120	0.820	0.030	0.090	0.030	0.100	0.060	0.260	0.420	0.820	0.280	0.020	0.020
Tribut	0.025	0.014	-0.017	0.012	-0.005	0.005	-0.067	-0.012	-0.051	0.025	0.043	-0.027	-0.062	0.043	0.012	-0.037	-0.035	-0.024	0.021	-0.005	-0.045	0.040	-0.043	0.043
P	0.400	0.840	0.760	0.640	0.960	0.880	0.020	0.620	0.240	0.310	0.240	0.440	0.060	0.270	0.450	0.280	0.360	0.420	0.540	0.820	0.120	0.220	0.180	0.180
Size	0.028	0.032	-0.033	0.028	-0.004	0.033	-0.001	0.039	0.032	-0.036	0.011	-0.044	-0.049	0.011	-0.016	0.007	0.037	0.008	0.024	-0.018	0.013	0.047	-0.011	0.011
P	0.340	0.400	0.380	0.500	0.900	0.380	0.860	0.220	0.460	0.450	0.460	0.200	0.120	1.000	1.000	1.000	0.380	0.700	0.480	0.500	0.640	0.120	0.840	0.840
Rip	0.003	0.008	-0.005	-0.030	0.022	-0.008	0.011	0.027	0.018	-0.009	-0.016	0.023	0.019	-0.016	0.013	-0.002	0.022	0.033	-0.023	0.018	0.037	-0.021	0.016	-0.016
P	0.900	0.860	0.960	0.560	0.560	0.860	0.820	0.340	0.900	0.900	0.900	0.620	0.500	0.900	0.900	0.900	0.680	0.240	0.480	0.580	0.180	0.560	0.600	0.600
S1	-0.002	-0.006	0.004	0.029	-0.021	0.008	-0.012	-0.026	-0.018	0.008	0.017	-0.023	-0.019	0.017	-0.013	0.001	-0.021	-0.034	0.023	-0.018	-0.037	0.021	-0.017	0.017
P	0.920	0.880	1.000	0.560	0.600	0.860	0.820	0.340	0.870	0.870	0.870	0.620	0.520	0.870	0.870	0.870	0.680	0.220	0.480	0.580	0.180	0.560	0.580	0.580
S3	0.010	0.016	-0.016	0.018	-0.003	0.010	-0.023	-0.016	-0.011	-0.005	0.030	-0.017	-0.014	0.030	-0.010	-0.009	-0.012	-0.032	0.023	-0.021	-0.024	0.026	-0.030	0.030
P	0.740	0.760	0.760	0.640	0.920	0.840	0.640	0.580	0.780	0.780	0.420	0.700	0.760	0.420	0.800	0.800	0.800	0.200	0.400	0.620	0.340	0.380	0.280	0.280
S4	-0.001	-0.003	0.001	0.028	-0.019	0.008	-0.013	-0.026	-0.017	0.006	0.019	-0.022	-0.018	0.019	-0.013	0.000	-0.020	-0.035	0.023	-0.019	-0.035	0.022	-0.019	0.019
P	0.980	0.960	1.000	0.560	0.660	0.820	0.840	0.340	0.780	0.780	0.780	0.640	0.580	0.780	0.780	0.780	0.700	0.240	0.460	0.620	0.260	0.520	0.520	0.520
S5	0.003	0.007	-0.005	-0.029	0.022	-0.008	0.011	0.026	0.018	-0.009	-0.016	0.023	0.019	-0.016	0.013	-0.002	0.022	0.034	-0.023	0.018	0.037	-0.021	0.016	-0.016
P	0.920	0.860	0.960	0.560	0.580	0.860	0.820	0.340	0.870	0.870	0.870	0.620	0.500	0.870	0.870	0.870	0.680	0.220	0.480	0.580	0.180	0.560	0.580	0.580
S8	0.003	0.008	-0.006	-0.030	0.023	-0.008	0.011	0.027	0.018	-0.009	-0.015	0.024	0.020	-0.015	0.013	-0.002	0.022	0.033	-0.023	0.017	0.037	-0.020	0.015	-0.015
P	0.900	0.860	0.940	0.560	0.560	0.880	0.820	0.340	0.900	0.900	0.900	0.620	0.500	0.900	0.900	0.900	0.680	0.240	0.500	0.580	0.180	0.560	0.600	0.600
U1	0.002	0.006	-0.004	-0.029	0.021	-0.008	0.012	0.026	0.018	-0.008	-0.017	0.023	0.019	-0.017	0.013	-0.001	0.021	0.034	-0.023	0.018	0.036	-0.021	0.017	-0.017
P	0.920	0.880	1.000	0.560	0.620	0.860	0.840	0.340	0.870	0.870	0.870	0.620	0.540	0.870	0.870	0.870	0.680	0.220	0.480	0.580	0.180	0.560	0.580	0.580
U2	-0.002	-0.006	0.004	0.029	-0.021	0.008	-0.012	-0.026	-0.018	0.008	0.017	-0.023	-0.019	0.017	-0.013	0.001	-0.021	-0.034	0.023	-0.018	-0.037	0.021	-0.017	0.017
P	0.920	0.880	1.000	0.560	0.600	0.860	0.820	0.340	0.870	0.870	0.870	0.620	0.520	0.870	0.870	0.870	0.680	0.220	0.480	0.580	0.180	0.560	0.580	0.580
U3	0.006	0.017	-0.015	-0.033	0.028	-0.007	0.006	0.028	0.020	-0.015	-0.007	0.026	0.023	-0.007	0.013	-0.007	0.025	0.030	-0.022	0.015	0.040	-0.018	0.007	-0.007
P	0.820	0.640	0.700	0.480	0.420	0.820	1.000	0.300	0.960	0.960	0.960	0.560	0.380	1.000	1.000	1.000	0.640	0.300	0.520	0.580	0.100	0.520	0.860	0.860
U4	-0.002	-0.005	0.003	0.029	-0.021	0.008	-0.012	-0.026	-0.018	0.008	0.017	-0.023	-0.019	0.017	-0.013	0.001	-0.021	-0.034	0.023	-0.018	-0.036	0.021	-0.017	0.017
P	0.940	0.900	1.000	0.560	0.640	0.860	0.840	0.340	0.870	0.870	0.870	0.620	0.540	0.870	0.870	0.870	0.680	0.240	0.480	0.580	0.180	0.560	0.580	0.580
Tree	-0.002	-0.006	0.004	0.029	-0.022	0.008	-0.012	-0.026	-0.018	0.008	0.016	-0.023	-0.019	0.016	-0.013	0.001	-0.021	-0.034	0.023	-0.018	-0.037	0.021	-0.016	0.016
P	0.920	0.880	0.980	0.560	0.600	0.860	0.820	0.340	0.870	0.870	0.870	0.620	0.520	0.870	0.870	0.870	0.680	0.220	0.480	0.580	0.180	0.560	0.580	0.580

Table A.5 Correlations from the fourth-corner analysis between species traits and environmental variables at the very broad spatial scale in Lac Paré. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	-0.112	0.004	0.000	-0.016	-0.078	0.018	-0.027	-0.027	-0.033	0.041	-0.016	-0.003	-0.022	-0.016	0.000	0.016	-0.048	0.042	-0.020	-0.005	-0.039	-0.011	0.041	-0.041
P	0.024	0.988	1.000	0.774	0.144	0.744	0.624	0.652	0.564	0.564	0.564	0.934	0.626	0.746	0.000	0.746	0.442	0.390	0.708	0.924	0.420	0.748	0.414	0.414
Z	-0.070	-0.034	0.029	-0.020	-0.044	0.048	0.022	-0.049	-0.040	0.055	-0.030	-0.024	-0.021	-0.030	0.000	0.030	-0.045	0.044	-0.049	0.007	-0.054	-0.008	0.025	-0.025
P	0.196	0.472	0.590	0.694	0.448	0.274	0.640	0.406	0.410	0.309	0.410	0.584	0.634	0.500	0.000	0.500	0.436	0.332	0.250	0.874	0.226	0.812	0.594	0.594
Emerg	0.005	-0.011	0.025	-0.036	0.010	-0.031	-0.029	-0.052	-0.053	-0.010	0.098	0.050	0.056	0.098	0.000	-0.098	-0.043	-0.039	0.033	0.022	0.009	0.010	-0.102	0.102
P	0.918	0.868	0.656	0.426	0.868	0.566	0.540	0.392	0.280	0.424	0.102	0.308	0.264	0.068	0.000	0.068	0.448	0.468	0.524	0.610	0.872	0.796	0.058	0.058
Subm	0.036	-0.008	0.013	-0.044	0.029	0.044	0.003	-0.037	-0.042	0.000	0.064	-0.004	0.024	0.064	0.000	-0.064	-0.005	-0.003	-0.032	0.041	-0.007	0.044	-0.098	0.098
P	0.512	0.894	0.792	0.370	0.624	0.332	0.938	0.520	0.372	0.514	0.363	0.896	0.656	0.242	0.000	0.242	0.890	1.000	0.456	0.356	0.830	0.300	0.070	0.070
Cover	0.061	0.004	-0.020	0.055	0.056	0.041	0.009	0.037	0.014	0.025	-0.062	-0.071	-0.066	-0.062	0.000	0.062	0.040	0.029	-0.035	0.021	-0.029	0.022	0.054	-0.054
P	0.250	0.936	0.692	0.298	0.304	0.418	0.914	0.524	0.606	0.606	0.414	0.166	0.206	0.276	0.000	0.276	0.482	0.558	0.488	0.658	0.552	0.642	0.340	0.340
Fetch	-0.004	-0.079	0.064	0.047	-0.048	0.042	0.110	0.009	-0.025	0.047	-0.041	-0.067	-0.056	-0.041	0.000	0.041	0.018	0.037	-0.049	0.063	-0.042	-0.034	0.027	-0.027
P	0.928	0.112	0.228	0.352	0.398	0.410	0.036	0.886	0.468	0.468	0.468	0.186	0.266	0.464	0.000	0.464	0.772	0.450	0.314	0.158	0.378	0.432	0.600	0.600
Tribut	-0.030	-0.061	0.030	0.020	0.038	-0.002	0.059	-0.054	-0.040	0.056	-0.031	-0.013	-0.016	-0.030	0.000	0.031	-0.056	0.006	-0.003	-0.003	-0.053	-0.017	0.033	-0.033
P	0.574	0.232	0.530	0.722	0.476	0.938	0.276	0.332	0.394	0.378	0.394	0.838	0.800	0.642	0.000	0.642	0.308	0.902	0.962	0.940	0.278	0.718	0.598	0.598
Size	-0.068	-0.075	0.058	0.004	0.009	0.007	0.044	-0.081	-0.024	0.089	-0.110	-0.008	-0.017	-0.110	0.000	0.110	-0.088	0.037	-0.028	-0.045	-0.074	-0.086	0.115	-0.115
P	0.202	0.128	0.254	0.988	0.910	0.866	0.392	0.184	0.310	0.087	0.087	0.862	0.730	0.058	0.000	0.058	0.144	0.418	0.538	0.288	0.106	0.080	0.032	0.032
Rip	-0.084	0.022	-0.015	-0.031	-0.040	0.014	-0.035	-0.016	-0.016	0.030	-0.024	0.011	-0.016	-0.024	0.000	0.024	-0.045	0.051	-0.020	-0.021	-0.025	-0.027	0.058	-0.058
P	0.140	0.710	0.800	0.546	0.404	0.798	0.536	0.794	0.849	0.849	0.849	0.822	0.748	0.638	0.000	0.638	0.464	0.306	0.706	0.626	0.654	0.618	0.280	0.280
S1	0.084	-0.022	0.013	0.031	0.042	-0.013	0.036	0.016	0.017	-0.029	0.022	-0.012	0.015	0.022	0.000	-0.022	0.045	-0.050	0.019	0.021	0.025	0.026	-0.056	0.056
P	0.140	0.716	0.830	0.546	0.388	0.810	0.526	0.796	0.870	0.870	0.870	0.812	0.762	0.660	0.000	0.660	0.460	0.318	0.726	0.632	0.668	0.632	0.292	0.292
S3	-0.084	0.023	-0.015	-0.031	-0.039	0.014	-0.035	-0.016	-0.016	0.030	-0.025	0.010	-0.016	-0.025	0.000	0.025	-0.045	0.052	-0.021	-0.021	-0.025	-0.027	0.059	-0.059
P	0.138	0.700	0.788	0.544	0.428	0.798	0.544	0.796	0.837	0.837	0.837	0.826	0.738	0.622	0.000	0.622	0.466	0.302	0.690	0.628	0.654	0.612	0.272	0.272
S4	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	1.000	0.564	1.000	1.000	1.000	0.818	1.000	1.000	1.000	1.000	1.000	0.756	1.000	0.794	0.000	0.794	1.000	0.378	1.000	1.000	1.000	1.000	1.000	1.000
S5	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	1.000	0.564	1.000	1.000	1.000	0.818	1.000	1.000	1.000	1.000	1.000	0.756	1.000	0.794	0.000	0.794	1.000	0.378	1.000	1.000	1.000	1.000	1.000	1.000
S8	-0.083	0.025	-0.025	-0.029	-0.018	0.019	-0.029	-0.014	-0.011	0.034	-0.040	0.005	-0.021	-0.040	0.000	0.040	-0.042	0.058	-0.028	-0.024	-0.028	-0.036	0.072	-0.072
P	0.126	0.650	0.648	0.588	0.684	0.726	0.614	0.852	0.681	0.681	0.681	0.946	0.670	0.454	0.000	0.454	0.494	0.236	0.588	0.590	0.602	0.476	0.198	0.198
U1	-0.084	0.022	-0.013	-0.031	-0.043	0.013	-0.036	-0.016	-0.017	0.029	-0.022	0.012	-0.015	-0.022	0.000	0.022	-0.045	0.050	-0.019	-0.021	-0.024	-0.025	0.055	-0.055
P	0.142	0.722	0.838	0.544	0.374	0.810	0.522	0.796	0.867	0.867	0.867	0.806	0.760	0.664	0.000	0.664	0.460	0.322	0.734	0.640	0.674	0.634	0.296	0.296
U2	0.083	-0.021	0.012	0.032	0.044	-0.012	0.036	0.016	0.017	-0.028	0.021	-0.012	0.014	0.021	0.000	-0.021	0.045	-0.049	0.018	0.021	0.024	0.025	-0.054	0.054
P	0.140	0.726	0.852	0.540	0.358	0.828	0.516	0.796	0.873	0.873	0.873	0.800	0.774	0.670	0.000	0.670	0.462	0.330	0.736	0.634	0.678	0.634	0.306	0.306
U3	-0.084	0.023	-0.017	-0.031	-0.035	0.015	-0.034	-0.015	-0.016	0.031	-0.027	0.009	-0.018	-0.027	0.000	0.027	-0.044	0.053	-0.022	-0.022	-0.026	-0.029	0.061	-0.061
P	0.130	0.686	0.758	0.562	0.462	0.782	0.552	0.806	0.822	0.822	0.822	0.858	0.728	0.598	0.000	0.598	0.466	0.280	0.674	0.626	0.634	0.582	0.258	0.258
U4	0.082	-0.020	0.008	0.032	0.050	-0.010	0.038	0.017	0.018	-0.026	0.016	-0.015	0.011	0.016	0.000	-0.016	0.045	-0.045	0.015	0.021	0.022	0.022	-0.049	0.049
P	0.152	0.748	0.904	0.530	0.300	0.866	0.490	0.788	0.957	0.957	0.957	0.762	0.838	0.766	0.000	0.766	0.450	0.376	0.776	0.630	0.696	0.678	0.360	0.360
Tree	0.084	-0.022	0.014	0.031	0.041	-0.013	0.035	0.016	0.016	-0.029	0.023	-0.011	0.015	0.023	0.000	-0.023	0.045	-0.050	0.020	0.021	0.025	0.026	-0.057	0.057
P	0.140	0.716	0.820	0.554	0.392	0.808	0.530	0.788	0.855	0.855	0.855	0.820	0.754	0.652	0.000	0.652	0.462	0.310	0.714	0.628	0.666	0.628	0.290	0.290

Table A.6 Correlations from the fourth-corner analysis between species traits and environmental variables at the broad spatial scale in Lac Paré. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.081	0.091	-0.119	0.056	0.060	0.001	0.041	0.172	0.107	-0.096	-0.004	-0.040	-0.045	-0.004	0.000	0.004	0.159	-0.004	0.012	0.021	0.088	0.050	0.012	-0.012
P	0.122	0.040	0.010	0.280	0.274	1.000	0.374	0.004	0.054	0.054	0.495	0.460	0.402	0.990	0.000	0.990	0.008	0.918	0.814	0.662	0.076	0.260	0.876	0.876
Z	-0.021	-0.049	0.074	-0.012	-0.087	0.014	-0.005	-0.051	-0.062	0.047	0.018	-0.003	-0.021	0.018	0.000	-0.018	-0.070	0.023	0.000	-0.008	-0.056	0.055	0.008	-0.008
P	0.748	0.312	0.152	0.778	0.102	0.754	0.922	0.362	0.336	0.336	0.349	0.954	0.632	0.698	0.000	0.698	0.230	0.630	0.988	0.832	0.226	0.236	0.904	0.904
Emerg	0.027	0.037	-0.034	0.013	0.015	-0.023	-0.042	0.027	0.007	-0.029	0.037	0.009	0.002	0.037	0.000	-0.037	0.019	-0.023	0.032	0.002	0.022	0.039	-0.026	0.026
P	0.588	0.436	0.478	0.772	0.702	0.662	0.406	0.618	0.798	0.798	0.798	0.870	0.974	0.532	0.000	0.532	0.696	0.658	0.550	0.972	0.614	0.456	0.642	0.642
Subm	-0.003	-0.006	-0.006	-0.006	0.026	0.014	-0.003	-0.031	0.003	0.028	-0.051	-0.007	-0.017	-0.051	0.000	0.051	-0.041	0.012	0.000	-0.065	-0.037	0.057	0.062	-0.062
P	0.996	0.900	0.932	0.884	0.616	0.754	0.970	0.570	0.566	0.566	0.528	0.858	0.726	0.352	0.000	0.352	0.488	0.784	1.000	0.138	0.448	0.230	0.246	0.246
Cover	-0.053	-0.043	0.050	0.022	-0.084	0.066	0.003	-0.031	-0.069	0.099	-0.058	-0.068	-0.096	-0.058	0.000	0.058	-0.063	0.089	-0.056	0.015	-0.105	0.034	0.093	-0.093
P	0.326	0.352	0.318	0.648	0.114	0.160	0.950	0.576	0.170	0.063	0.170	0.150	0.048	0.298	0.000	0.298	0.276	0.066	0.224	0.710	0.034	0.484	0.076	0.076
Fetch	-0.005	0.011	0.002	-0.017	-0.038	-0.035	0.013	0.027	0.021	-0.055	0.060	0.040	0.040	0.060	0.000	-0.060	0.027	-0.036	0.037	-0.001	0.054	0.010	-0.057	0.057
P	0.902	0.884	0.940	0.666	0.454	0.420	0.754	0.688	0.345	0.342	0.342	0.344	0.322	0.234	0.000	0.234	0.670	0.434	0.396	0.976	0.242	0.804	0.268	0.268
Tribut	-0.059	-0.048	0.064	-0.037	-0.059	0.063	0.009	-0.068	-0.046	0.086	-0.071	-0.025	-0.036	-0.071	0.000	0.071	-0.079	0.081	-0.069	-0.018	-0.081	-0.031	0.083	-0.083
P	0.264	0.340	0.240	0.452	0.260	0.180	0.852	0.248	0.220	0.084	0.220	0.624	0.464	0.220	0.000	0.220	0.188	0.088	0.154	0.676	0.082	0.534	0.142	0.142
Size	-0.087	-0.021	0.040	-0.053	-0.049	0.083	-0.055	-0.095	-0.074	0.113	-0.074	-0.029	-0.051	-0.074	0.000	0.074	-0.117	0.105	-0.080	-0.031	-0.114	0.002	0.100	-0.100
P	0.120	0.644	0.422	0.274	0.318	0.086	0.312	0.110	0.136	0.018	0.136	0.508	0.258	0.168	0.000	0.168	0.058	0.032	0.084	0.484	0.014	0.974	0.070	0.070
Rip	-0.003	0.002	0.011	-0.033	-0.021	0.000	0.010	0.001	0.045	-0.019	-0.037	0.023	0.025	-0.037	0.000	0.037	0.004	0.002	-0.004	-0.052	0.022	-0.018	0.032	-0.032
P	0.942	0.920	0.810	0.446	0.680	1.000	0.898	0.986	0.570	0.570	0.570	0.616	0.604	0.518	0.000	0.518	0.972	0.960	0.944	0.208	0.634	0.736	0.582	0.582
S1	0.000	0.008	0.005	-0.033	-0.017	0.001	0.009	0.007	0.049	-0.023	-0.038	0.023	0.024	-0.038	0.000	0.038	0.009	0.003	-0.005	-0.054	0.026	-0.017	0.034	-0.034
P	1.000	0.854	0.894	0.448	0.724	0.948	0.904	0.900	0.477	0.514	0.514	0.622	0.614	0.514	0.000	0.514	0.878	0.944	0.930	0.194	0.584	0.736	0.548	0.548
S3	0.000	0.007	0.006	-0.033	-0.017	0.000	0.009	0.006	0.049	-0.022	-0.038	0.023	0.024	-0.038	0.000	0.038	0.008	0.003	-0.005	-0.054	0.025	-0.017	0.034	-0.034
P	0.980	0.860	0.882	0.450	0.720	0.950	0.904	0.900	0.486	0.514	0.514	0.620	0.608	0.514	0.000	0.514	0.882	0.940	0.938	0.192	0.590	0.734	0.548	0.548
S4	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.862	0.884	1.000	0.606	0.394	0.802	1.000	1.000	0.393	0.692	0.835	1.000	1.000	1.000	0.000	1.000	1.000	1.000	1.000	0.126	1.000	0.404	0.198	0.198
S5	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.862	0.884	1.000	0.606	0.394	0.802	1.000	1.000	0.393	0.692	0.835	1.000	1.000	1.000	0.000	1.000	1.000	1.000	1.000	0.126	1.000	0.404	0.198	0.198
S8	-0.053	-0.075	0.062	0.045	-0.043	0.017	0.021	-0.063	-0.116	0.087	0.034	-0.045	-0.049	0.034	0.000	-0.034	-0.067	0.020	-0.015	0.082	-0.088	0.006	-0.025	0.025
P	0.346	0.140	0.262	0.310	0.444	0.838	0.730	0.304	0.027	0.054	0.255	0.304	0.282	0.510	0.000	0.510	0.246	0.744	0.838	0.042	0.054	0.788	0.630	0.630
U1	0.000	-0.007	-0.006	0.033	0.017	-0.001	-0.009	-0.007	-0.049	0.022	0.038	-0.023	-0.024	0.038	0.000	-0.038	-0.008	-0.003	0.005	0.054	-0.025	0.017	-0.033	0.034
P	1.000	0.854	0.884	0.450	0.720	0.950	0.902	0.900	0.483	0.514	0.514	0.622	0.610	0.514	0.000	0.514	0.882	0.942	0.936	0.194	0.588	0.734	0.550	0.550
U2	-0.001	0.006	0.007	-0.033	-0.018	0.000	0.009	0.006	0.048	-0.022	-0.038	0.023	0.024	-0.038	0.000	0.038	0.007	0.002	-0.005	-0.054	0.025	-0.017	0.033	-0.033
P	0.974	0.868	0.874	0.452	0.710	0.950	0.902	0.918	0.501	0.514	0.514	0.620	0.606	0.514	0.000	0.514	0.896	0.946	0.938	0.194	0.596	0.738	0.554	0.554
U3	-0.001	0.006	0.007	-0.033	-0.018	0.000	0.009	0.006	0.048	-0.022	-0.038	0.023	0.024	-0.038	0.000	0.038	0.007	0.002	-0.005	-0.054	0.025	-0.017	0.034	-0.033
P	0.972	0.868	0.874	0.452	0.710	0.950	0.900	0.916	0.498	0.514	0.514	0.620	0.606	0.514	0.000	0.514	0.898	0.946	0.938	0.192	0.596	0.738	0.552	0.552
U4	-0.004	-0.014	0.001	0.034	0.013	-0.002	-0.007	-0.014	-0.054	0.027	0.038	-0.022	-0.023	0.038	0.000	-0.038	-0.015	-0.004	0.006	0.054	-0.030	0.015	-0.034	0.034
P	0.944	0.764	1.000	0.426	0.770	0.930	0.924	0.804	0.417	0.510	0.510	0.640	0.608	0.510	0.000	0.510	0.804	0.932	0.896	0.198	0.514	0.756	0.538	0.538
Tree	-0.001	-0.009	-0.004	0.034	0.016	-0.001	-0.009	-0.008	-0.050	0.024	0.038	-0.023	-0.024	0.038	0.000	-0.038	-0.010	-0.003	0.005	0.054	-0.027	0.017	-0.034	0.034
P	0.990	0.826	0.904	0.438	0.738	0.940	0.908	0.884	0.468	0.518	0.518	0.632	0.614	0.518	0.000	0.518	0.856	0.942	0.926	0.194	0.572	0.742	0.544	0.544

Table A.7 Correlations from the fourth-corner analysis between species traits and environmental variables at the meso spatial scale in Lac Paré. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	-0.017	-0.010	0.003	0.070	-0.032	0.011	-0.030	0.008	-0.042	0.040	-0.003	-0.058	-0.052	-0.003	0.000	0.003	0.012	0.008	-0.013	0.073	-0.039	-0.009	-0.003	0.003
P	0.772	0.904	1.000	0.178	0.574	0.734	0.550	0.940	0.576	0.576	0.576	0.236	0.266	1.000	0.000	1.000	0.842	0.824	0.710	0.090	0.408	0.874	0.922	0.922
Z	-0.092	-0.040	0.018	0.070	-0.066	0.055	0.006	-0.020	-0.040	0.106	-0.114	-0.093	-0.103	-0.114	0.000	0.114	-0.033	0.071	-0.059	0.023	-0.102	-0.022	0.123	-0.123
P	0.106	0.440	0.764	0.162	0.226	0.242	0.916	0.742	0.206	0.021	0.034	0.036	0.026	0.034	0.000	0.034	0.574	0.150	0.216	0.568	0.016	0.680	0.028	0.028
Emerg	0.058	-0.024	0.047	-0.015	-0.003	-0.084	0.004	-0.016	-0.018	-0.067	0.139	0.078	0.088	0.139	0.000	-0.139	-0.002	-0.099	0.089	0.016	0.063	0.026	-0.147	0.147
P	0.262	0.606	0.342	0.744	0.932	0.086	0.960	0.754	0.350	0.116	0.015	0.092	0.074	0.010	0.000	0.010	0.938	0.046	0.064	0.738	0.136	0.596	0.010	0.010
Subm	-0.043	-0.045	0.072	-0.075	-0.050	0.025	0.002	-0.087	-0.069	0.047	0.029	0.032	0.019	0.029	0.000	-0.029	-0.098	0.036	-0.022	-0.019	-0.048	0.010	-0.010	0.010
P	0.468	0.380	0.182	0.138	0.372	0.592	0.904	0.128	0.276	0.340	0.340	0.536	0.736	0.646	0.000	0.646	0.076	0.460	0.622	0.696	0.326	0.874	0.916	0.916
Cover	-0.090	-0.103	0.092	0.007	-0.084	0.036	0.087	-0.072	-0.032	0.101	-0.118	-0.033	-0.058	-0.118	0.000	0.118	-0.097	0.063	-0.034	-0.067	-0.102	0.003	0.145	-0.145
P	0.098	0.044	0.100	0.830	0.126	0.464	0.070	0.240	0.284	0.051	0.051	0.492	0.238	0.034	0.000	0.034	0.102	0.200	0.486	0.136	0.040	0.990	0.016	0.016
Fetch	-0.075	-0.052	0.020	0.126	-0.070	-0.014	0.016	0.005	-0.024	0.065	-0.070	-0.077	-0.076	-0.070	0.000	0.070	0.004	-0.008	0.009	0.042	-0.062	-0.020	0.067	-0.067
P	0.182	0.308	0.692	0.010	0.196	0.782	0.796	0.946	0.291	0.264	0.264	0.108	0.094	0.196	0.000	0.196	0.986	0.884	0.862	0.308	0.202	0.702	0.200	0.200
Tribut	-0.098	-0.095	0.073	0.002	-0.066	0.021	0.110	-0.059	-0.004	0.076	-0.119	-0.018	-0.035	-0.119	0.000	0.119	-0.077	0.044	-0.024	-0.077	-0.074	-0.015	0.136	-0.136
P	0.066	0.060	0.162	0.936	0.196	0.678	0.040	0.328	0.474	0.114	0.054	0.698	0.472	0.036	0.000	0.036	0.200	0.392	0.638	0.060	0.130	0.652	0.020	0.020
Size	0.048	0.088	-0.068	-0.029	0.048	-0.059	-0.102	0.032	0.033	-0.086	0.091	0.067	0.068	0.091	0.000	-0.091	0.034	-0.064	0.063	-0.012	0.082	0.024	-0.090	0.090
P	0.380	0.076	0.228	0.546	0.400	0.258	0.038	0.588	0.270	0.117	0.117	0.164	0.156	0.110	0.000	0.110	0.580	0.228	0.226	0.786	0.086	0.572	0.108	0.108
Rip	0.045	0.053	-0.020	-0.113	0.047	0.033	-0.042	-0.015	0.012	-0.027	0.027	0.053	0.040	0.027	0.000	-0.027	-0.028	0.038	-0.025	-0.055	0.023	0.028	-0.010	0.010
P	0.400	0.326	0.702	0.016	0.382	0.464	0.446	0.798	0.855	0.855	0.855	0.292	0.458	0.704	0.000	0.704	0.664	0.410	0.578	0.210	0.616	0.596	0.908	0.908
S1	-0.026	-0.032	-0.001	0.104	-0.023	-0.013	0.037	0.032	-0.005	0.020	-0.026	-0.062	-0.045	-0.026	0.000	0.026	0.048	-0.023	0.005	0.069	-0.015	-0.031	0.004	-0.004
P	0.650	0.564	0.968	0.026	0.658	0.758	0.500	0.606	0.993	0.993	0.993	0.204	0.368	0.722	0.000	0.722	0.414	0.602	0.896	0.126	0.750	0.540	0.998	0.998
S3	0.045	0.052	-0.019	-0.112	0.046	0.032	-0.042	-0.016	0.012	-0.027	0.027	0.053	0.040	0.027	0.000	-0.027	-0.028	0.037	-0.024	-0.055	0.023	0.028	-0.010	0.010
P	0.402	0.326	0.708	0.016	0.384	0.468	0.446	0.796	0.858	0.858	0.858	0.288	0.458	0.704	0.000	0.704	0.656	0.412	0.582	0.206	0.616	0.592	0.910	0.910
S4	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.983	0.976	0.980	1.000	0.939	1.000	1.000	1.000	1.000	1.000	1.000	0.790	0.496	1.000	0.000	1.000	0.894	1.000	0.306	1.000	0.811	0.940	0.780	0.780
S5	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.983	0.976	0.980	1.000	0.939	1.000	1.000	1.000	1.000	1.000	1.000	0.790	0.496	1.000	0.000	1.000	0.894	1.000	0.306	1.000	0.811	0.940	0.780	0.780
S8	0.020	0.013	-0.053	0.080	0.059	0.070	0.023	0.054	0.007	0.043	-0.081	-0.112	-0.090	-0.081	0.000	0.081	0.074	0.051	-0.078	0.083	-0.037	-0.036	0.051	-0.051
P	0.658	0.732	0.326	0.094	0.296	0.096	0.736	0.354	0.446	0.404	0.243	0.012	0.056	0.162	0.000	0.162	0.170	0.292	0.074	0.058	0.484	0.698	0.404	0.404
U1	0.043	0.050	-0.018	-0.112	0.044	0.031	-0.041	-0.017	0.011	-0.027	0.027	0.053	0.040	0.027	0.000	-0.027	-0.030	0.036	-0.023	-0.056	0.022	0.029	-0.009	0.009
P	0.420	0.352	0.730	0.018	0.406	0.480	0.462	0.782	0.870	0.870	0.870	0.282	0.450	0.706	0.000	0.706	0.618	0.422	0.610	0.198	0.624	0.580	0.908	0.908
U2	0.046	0.053	-0.021	-0.113	0.047	0.033	-0.042	-0.015	0.012	-0.028	0.027	0.052	0.040	0.027	0.000	-0.027	-0.027	0.038	-0.025	-0.054	0.023	0.028	-0.010	0.010
P	0.398	0.316	0.694	0.016	0.378	0.462	0.446	0.806	0.843	0.843	0.843	0.298	0.460	0.704	0.000	0.704	0.676	0.404	0.568	0.212	0.614	0.596	0.900	0.900
U3	-0.036	-0.042	0.009	0.108	-0.035	-0.023	0.039	0.023	-0.009	0.024	-0.027	-0.058	-0.043	-0.027	0.000	0.027	0.038	-0.031	0.015	0.062	-0.019	-0.030	0.007	-0.007
P	0.534	0.444	0.864	0.022	0.506	0.598	0.496	0.692	0.915	0.915	0.915	0.246	0.422	0.714	0.000	0.714	0.526	0.492	0.716	0.154	0.678	0.562	0.942	0.942
U4	-0.041	-0.048	0.016	0.111	-0.042	-0.029	0.041	0.018	-0.011	0.026	-0.027	-0.054	-0.041	-0.027	0.000	0.027	0.032	-0.035	0.021	0.058	-0.021	-0.029	0.009	-0.009
P	0.454	0.376	0.772	0.018	0.442	0.510	0.466	0.764	0.885	0.885	0.885	0.274	0.444	0.716	0.000	0.716	0.594	0.440	0.640	0.190	0.632	0.580	0.918	0.918
Tree	0.047	0.054	-0.022	-0.112	0.050	0.035	-0.042	-0.013	0.013	-0.028	0.026	0.050	0.038	0.026	0.000	-0.026	-0.025	0.040	-0.027	-0.052	0.023	0.028	-0.010	0.010
P	0.376	0.316	0.672	0.016	0.366	0.448	0.448	0.832	0.831	0.831	0.831	0.320	0.476	0.716	0.000	0.716	0.706	0.396	0.544	0.228	0.618	0.602	0.896	0.896

Table A.8 Correlations from the fourth-corner analysis between species traits and environmental variables at the fine spatial scale in Lac Paré. Species traits codes are found in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Litt	0.056	0.080	-0.097	0.002	0.065	-0.046	0.016	0.103	0.084	-0.132	0.089	0.035	0.067	0.089	0.000	-0.089	0.136	-0.080	0.043	0.039	0.133	-0.006	-0.127	0.127
P	0.324	0.100	0.058	0.992	0.226	0.370	0.806	0.080	0.092	0.012	0.092	0.450	0.158	0.108	0.000	0.108	0.018	0.112	0.392	0.368	0.006	0.940	0.012	0.012
Z	-0.029	0.018	0.033	-0.114	-0.017	-0.060	-0.086	-0.080	-0.018	-0.050	0.110	0.127	0.144	0.110	0.000	-0.110	-0.055	-0.061	0.038	-0.018	0.064	-0.080	-0.131	0.131
P	0.618	0.734	0.536	0.026	0.788	0.196	0.094	0.158	0.364	0.268	0.060	0.008	0.004	0.040	0.000	0.040	0.344	0.204	0.412	0.660	0.160	0.088	0.020	0.020
Emerg	-0.062	-0.019	0.088	-0.137	-0.052	-0.049	-0.110	-0.147	-0.063	0.006	0.087	0.135	0.140	0.087	0.000	-0.087	-0.134	-0.033	0.024	-0.041	0.010	-0.093	-0.093	0.093
P	0.248	0.712	0.122	0.012	0.360	0.296	0.032	0.010	0.220	0.464	0.180	0.004	0.004	0.120	0.000	0.120	0.024	0.498	0.582	0.332	0.820	0.032	0.106	0.106
Subm	0.028	0.064	-0.055	-0.045	0.039	-0.057	-0.023	0.041	0.053	-0.114	0.108	0.077	0.106	0.108	0.000	-0.108	0.074	-0.082	0.047	0.021	0.121	-0.037	-0.143	0.143
P	0.620	0.208	0.264	0.364	0.476	0.256	0.648	0.474	0.144	0.030	0.038	0.094	0.030	0.038	0.000	0.038	0.224	0.094	0.352	0.654	0.014	0.450	0.006	0.006
Cover	-0.058	-0.081	0.100	-0.006	-0.066	0.045	-0.019	-0.108	-0.086	0.133	-0.087	-0.032	-0.063	-0.087	0.000	0.087	-0.140	0.080	-0.043	-0.041	-0.134	0.004	0.125	-0.125
P	0.300	0.098	0.048	0.940	0.218	0.390	0.748	0.066	0.084	0.012	0.084	0.490	0.182	0.118	0.000	0.118	0.016	0.118	0.398	0.354	0.006	0.992	0.014	0.014
Fetch	0.084	0.086	-0.136	0.066	0.087	-0.022	0.067	0.170	0.112	-0.131	0.046	-0.029	0.000	0.046	0.000	-0.046	0.195	-0.063	0.031	0.057	0.125	0.038	-0.080	0.080
P	0.146	0.082	0.008	0.162	0.086	0.634	0.218	0.006	0.024	0.015	0.193	0.558	1.000	0.386	0.000	0.386	0.004	0.206	0.512	0.184	0.012	0.400	0.126	0.126
Tribut	-0.084	-0.086	0.136	-0.068	-0.088	0.021	-0.069	-0.171	-0.112	0.131	-0.044	0.030	0.002	-0.044	0.000	0.044	-0.196	0.062	-0.031	-0.058	-0.125	-0.039	0.079	-0.079
P	0.148	0.086	0.008	0.152	0.084	0.648	0.206	0.006	0.024	0.015	0.205	0.530	0.998	0.410	0.000	0.410	0.004	0.212	0.518	0.182	0.012	0.390	0.140	0.140
Size	0.088	0.058	-0.133	0.133	0.083	0.024	0.114	0.194	0.103	-0.071	-0.040	-0.112	-0.101	-0.040	0.000	0.040	0.197	-0.009	-0.002	0.059	0.057	0.087	0.026	-0.026
P	0.106	0.262	0.018	0.008	0.126	0.628	0.034	0.002	0.054	0.128	0.249	0.020	0.046	0.498	0.000	0.498	0.002	0.874	0.964	0.160	0.238	0.056	0.662	0.662
Rip	0.024	0.061	-0.049	-0.051	0.035	-0.058	-0.028	0.032	0.048	-0.111	0.110	0.082	0.111	0.109	0.000	-0.110	0.065	-0.081	0.047	0.018	0.118	-0.041	-0.144	0.144
P	0.666	0.226	0.324	0.290	0.520	0.242	0.590	0.586	0.167	0.033	0.038	0.072	0.020	0.038	0.000	0.038	0.264	0.094	0.342	0.708	0.016	0.412	0.006	0.006
S1	0.008	0.042	-0.037	-0.046	0.026	-0.059	-0.005	0.024	0.050	-0.101	0.091	0.079	0.107	0.091	0.000	-0.091	0.056	-0.080	0.046	0.007	0.109	-0.048	-0.125	0.125
P	0.862	0.414	0.470	0.344	0.618	0.244	0.884	0.678	0.156	0.054	0.104	0.092	0.026	0.104	0.000	0.104	0.342	0.098	0.356	0.904	0.028	0.388	0.024	0.024
S3	0.023	0.060	-0.049	-0.051	0.035	-0.058	-0.028	0.031	0.048	-0.110	0.109	0.082	0.111	0.109	0.000	-0.109	0.065	-0.081	0.047	0.018	0.118	-0.041	-0.144	0.144
P	0.670	0.232	0.328	0.290	0.520	0.240	0.596	0.590	0.166	0.036	0.040	0.072	0.020	0.040	0.000	0.040	0.268	0.094	0.340	0.710	0.016	0.408	0.006	0.006
S4	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.972	0.978	0.992	1.000	0.931	1.000	1.000	1.000	1.000	1.000	1.000	0.828	0.526	1.000	0.000	1.000	0.920	1.000	0.352	1.000	0.810	0.932	0.806	0.806
S5	-0.001	-0.001	-0.002	-0.003	-0.001	-0.003	-0.003	0.000	0.001	-0.001	0.000	-0.001	-0.001	0.000	0.000	-0.003	0.000	-0.003	0.000	-0.003	-0.001	0.000	0.003	0.000
P	0.972	0.978	0.992	1.000	0.931	1.000	1.000	1.000	1.000	1.000	1.000	0.828	0.526	1.000	0.000	1.000	0.920	1.000	0.352	1.000	0.810	0.932	0.806	0.806
S8	-0.090	-0.089	0.081	0.010	-0.061	0.038	0.034	-0.093	-0.078	0.112	-0.066	-0.037	-0.047	-0.066	0.000	0.066	-0.102	0.053	-0.042	-0.003	-0.109	-0.021	0.076	-0.076
P	0.094	0.082	0.128	0.908	0.298	0.486	0.510	0.100	0.134	0.024	0.134	0.442	0.338	0.222	0.000	0.222	0.050	0.306	0.426	0.924	0.018	1.000	0.142	0.142
U1	0.026	0.063	-0.050	-0.051	0.036	-0.058	-0.031	0.033	0.047	-0.111	0.112	0.082	0.111	0.112	0.000	-0.112	0.066	-0.081	0.046	0.019	0.119	-0.040	-0.146	0.146
P	0.648	0.212	0.310	0.288	0.512	0.244	0.564	0.574	0.166	0.030	0.036	0.066	0.020	0.036	0.000	0.036	0.266	0.094	0.342	0.682	0.018	0.422	0.006	0.006
U2	-0.026	-0.063	0.050	0.051	-0.036	0.058	0.032	-0.033	-0.047	0.111	-0.112	-0.082	-0.111	-0.112	0.000	0.112	-0.066	0.081	-0.047	-0.019	-0.119	0.040	0.146	-0.146
P	0.644	0.214	0.310	0.288	0.514	0.242	0.556	0.574	0.168	0.033	0.036	0.066	0.020	0.036	0.000	0.036	0.266	0.094	0.346	0.678	0.018	0.420	0.006	0.006
U3	-0.024	-0.061	0.049	0.051	-0.035	0.058	0.029	-0.032	-0.047	0.111	-0.110	-0.082	-0.111	-0.110	0.000	0.110	-0.065	0.081	-0.047	-0.018	-0.118	0.041	0.144	-0.145
P	0.664	0.226	0.322	0.286	0.520	0.242	0.588	0.584	0.166	0.030	0.036	0.072	0.018	0.036	0.000	0.036	0.266	0.096	0.340	0.698	0.016	0.414	0.006	0.006
U4	0.021	0.058	-0.047	-0.051	0.034	-0.058	-0.025	0.030	0.048	-0.109	0.107	0.082	0.111	0.107	0.000	-0.107	0.064	-0.081	0.046	0.016	0.117	-0.043	-0.142	0.142
P	0.700	0.246	0.350	0.288	0.532	0.240	0.624	0.596	0.162	0.039	0.048	0.076	0.022	0.048	0.000	0.048	0.268	0.098	0.338	0.748	0.016	0.404	0.006	0.006
Tree	-0.026	-0.063	0.051	0.052	-0.037	0.058	0.031	-0.033	-0.047	0.112	-0.112	-0.082	-0.111	-0.112	0.000	0.112	-0.066	0.081	-0.046	-0.019	-0.119	0.040	0.146	-0.146
P	0.642	0.210	0.304	0.288	0.506	0.250	0.560	0.574	0.164	0.030	0.036	0.066	0.020	0.036	0.000	0.036	0.266	0.094	0.344	0.674	0.018	0.418	0.006	0.006

Chapitre 4

Effect of the spatial arrangement of habitat patches on the development of fish habitat models in the littoral zone of a Canadian Shield lake lake

A. Brind'Amour, D. Boisclair,

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ABSTRACT

We developed fish habitat models in a Canadian Shield lake using: i) a sampling-site approach based on analytical units having a surface area equal to that of sampling sites ($S \sim 200$ m^2), ii) a constant-multiple approach in which the analytical units constituted grouping of adjacent sampling sites in units of increasing sizes (e.g. 2S or 3S, etc), and iii) an habitat-patch approach in which only contiguous sampling sites with similar environmental characteristics were merged. The best models explaining within-lake variations of fish density, biomass, and community structure on the littoral zone were obtained using the constant-multiple approach but the predictive power of these models was highly variable ($0<R^2<0.9$) compared to the habitat-patch approach ($0.37<R^2<0.53$). For these approaches, intrinsic variables (variables estimated inside the analytical units) explained on average 16 to 27% of the variations of fish descriptors compared to 6 to 32% for extrinsic variables (variables observed outside analytical units or related to the spatial arrangement of habitat characteristics). Our study suggests that habitat patches are reliable analytical units to develop fish-habitat models. Our study also indicates that inclusion of variables that refer to landscape characteristics may significantly improve the predictive power of fish habitat models.

INTRODUCTION

Habitat loss is a main threat to the survival of fish species in lakes and rivers (Evans et al. 1996; Richter et al. 1997). For instance, perturbations affecting the littoral zone of lakes have been shown to cause a significant decline in fish productivity (Minns et al. 1996; Brazner and Beals 1997). Perturbations of littoral zones generally involve the replacement of areas of high structural heterogeneity related to the presence of woody debris and macrophytes by areas of lower heterogeneity like sandy beaches (Christensen et al. 1996; Radomski and Goeman 2001). Structural heterogeneity often shapes littoral zones in a mosaic of microhabitats suitable for spawning, nesting, foraging, and sheltering (Mittelbach 1981; Werner et al. 1983; Tabor and Wurtsbaugh 1991; Gafny et al. 1992). The presence of habitats that allow fish to perform most activities needed to complete their life cycles may explain the contribution of littoral zones to the biological productivity and diversity of lakes (Wetzel 1990; Schiemer and Zalewski 1992). Conservation programs therefore call for the development of habitat models that permit the identification of the features of littoral zones that should be protected and the prediction of the effect of perturbations on their fish communities (Brazner and Beals 1997).

Fish habitat models designed for littoral zones generally consist of relationships between fish community descriptors and environmental characteristics defined locally (Eadie and Keast 1984; Benson and Magnuson 1992; Bryan and Scarnecchia 1992; Gamboa-Pérez and Schmitter-Soto 1999). However, habitat variation exists over a range of spatial scales (Brind'Amour et al. 2005) and it may be important to identify the size of the units appropriate to test the existence of relationships between fish and habitat descriptors (Wiens 2002). Dependent and independent variables may be estimated within an area or a volume that corresponds to the sampling sites (S; *e.g.*: the area or the volume sampled by a seine; the size of a sampling quadrat). Hence, the size of the units used during the statistical analysis, the analytical units, may correspond to that of the sampling sites. This approach to develop habitat models is here defined as the 'sampling-site approach'. However, there are no indications that the size of the sampling sites, which is determined more by logistical constraints (the length of a seine; the opening of a trawl; the time required to survey a volume or surface area) than by ecological considerations, is optimal to model fish habitat quality (Poizat and Pont 1996). This situation may be explored by developing habitat models using analytical units that all constitute a same multiple of the sampling sites (e.g. 2S or 3 S, etc). This approach is further referred to as the 'constant-multiple approach'. Another approach may be to impose a spatial constraint to the procedure such that only contiguous sampling sites with similar environmental characteristics may be merged. This results in analytical units having a size potentially, but not necessarily, different from that of the sampling sites and from each other. Because these analytical units have homogeneous environmental characteristics, but yet, attributes different from their surroundings, they are defined as habitat patches (Wiens 1976). Hence, the development of habitat models based on the use of such analytical units is hereafter referred to as the 'habitat-patch approach'.

Fish habitat quality at one site may not be determined only by the environmental characteristics found within this site but also by conditions found in surrounding locations (Lewis et al. 1996; Kocik and Ferreri 1998). Although the study of the spatial arrangement of sites may contribute to the development of more powerful habitat models, few tests have been performed to assess the effect of the distance between two similar sites or the nature of neighbouring sites on fish habitat quality at a given location (Essington and Kitchell 1999). The objectives of our study were to test 1) the effect of the sampling-site, constant-multiple, and habitat-patch approaches on the predictive power of fish habitat models developed for the littoral zone of a lake and 2) the effect of variables that refer to the spatial arrangement of sites on these models.

MATERIALS AND METHODS

Study lake

Sampling was conducted in Lac Drouin (46°09'N, 73°55'W; Lanaudière Region of Québec, Canada; Figure 4.1). This Canadian Shield lake displays a diversified littoral zone with woody debris, rocky substrate, sand beaches, and patches of macrophytes of mixed species such as water shield (*Brasenia schreberi*), pipewort (*Eriocaulon aquaticum*), Eurasian water milfoil (*Myriophyllum spicatum*), and water lily (*Nymphea sp.*). It is a mesotrophic lake with a surface area of 31 ha, a maximum depth of 22 m, and a perimeter of 4.8 km. 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 ranges from 4°C to 8°C. The thermocline forms at 4.5 m depth in mid-June and breaks down in early October.

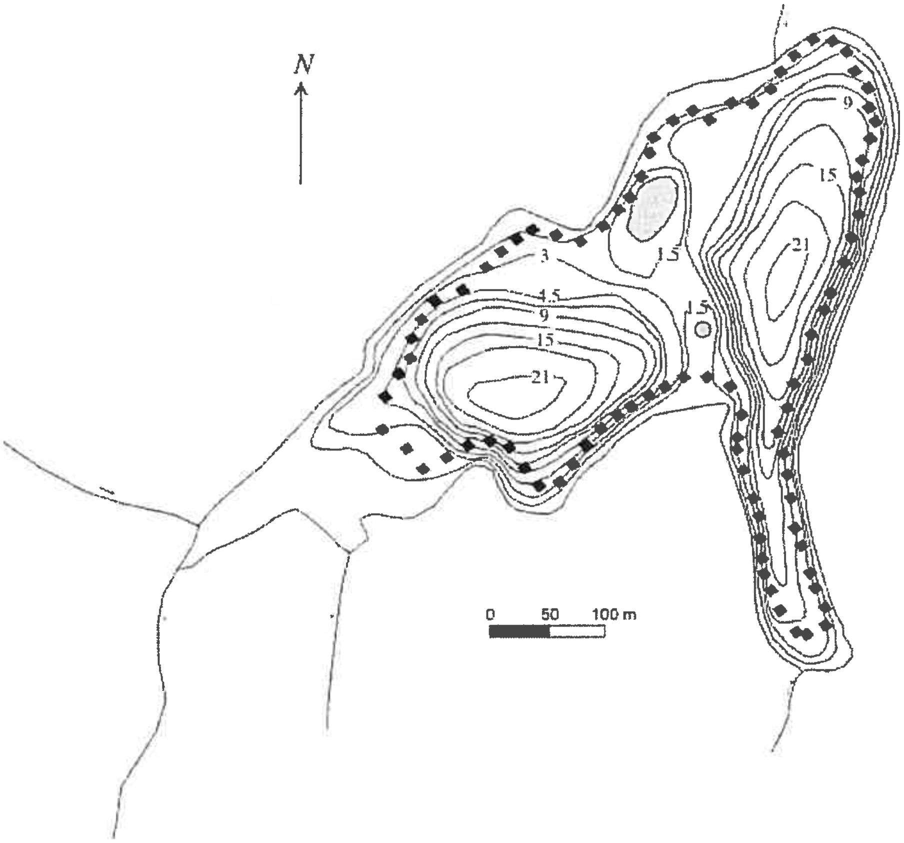

Figure 4.1 Map of Lac Drouin (Lanaudière. Québec). Black dots represent the 90 sampling sites in the littoral zone of the lake.

Sampling procedure

Fish community descriptors and environmental characteristics were quantified over 90 sites that covered the complete perimeter of the lake. Fish community descriptors were estimated three times at each site from 29 July to 4 August 2001. All environmental characteristics, with the exceptions of density of macrophytes and fetch, were noted at the end of May 2001. The density of macrophytes was quantified on 29 July 2001 and fetch was assessed on each day fish community descriptors were estimated. The length of a sampling site was defined by its shore length; the mean length was 53.9 m (SD = 13.2 m). The width of a sampling site 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 snorkelling. The mean width of a site was 10.5 m (range: 9 to 12 m). Geographical coordinates were estimated at each site using a global positioning system (Garmin - GPS 12) with a precision of ± 10 m. The perimeter of the lake was further separated in two sections comprising 48 (Section 1) and 42 sites (Section 2). These sections were surveyed during two consecutive days. This sampling procedure was used because a maximum of 50 sites could be surveyed within ~ 6 h (9h00 to 15h00). Sampling was limited to this time interval each day because local fish community descriptors may change among periods within a day (dawn, mid-day, dusk; Keast and Harker 1977). The sites from two consecutive days (i.e. two sections) were pooled in the same data file to represent the complete perimeter of the lake as a spatial continuum. The data of the three pairs of days that allowed us to obtain three complete perimeters were then added within homologous sites of the lake. This addition of the sections was done to minimize the effects of daily variations of fish community descriptors at each site. Justification for this procedure is given in (Brind'Amour et al. 2005).

Fish community descriptors

Surveys of the fish community were conducted using a modified version of the visual 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 approximately 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 approximately 10 $m \cdot min^{-1}$ to minimize fish disturbance (Eklöv 1997). The snorkellers noted their observations on plastic PVC rolls. They identified the species, the relative abundance, and the approximate size of the fish as they progressed. The relative abundance of fish was noted in six classes: 1 = 1 individual; 2 = 2 individuals; 3 = 3 individuals; 4 = 4-5 individuals; 5 = 6-9 individuals, and 6 = 10 individuals and more. Each fish was also categorized according to its size. The classification of fish size was based on specific ecological information extracted from Scott and Crossman (1973). This approach, applied to all fish species present in Lac Drouin, resulted in the creation of three size classes: SC_1 = shorter than 110 mm TL; SC_2 = 110-160 mm TL; SC_3= longer than 160 mm TL.

Computations

The fish community at each site was characterized using four descriptors: the total fish density (TFD), the relative fish biomass (RB), the size structure of the fish community, and the fish community composition. Since 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 discontinuous to continuous variables allowed us to compute the community descriptors. The relative biomass of fish for any combination of species and size class was estimated as:

$$\mathrm{RB} = \Sigma n_{i,s} \times M_{i,s} \quad (1)$$

where $n_{i,s}$ is the number of fish per species per size class and $W_{i,s}$ is the average fish mass (grams) per species per size class estimated using the length-mass relationships published in Schneider et al. (2000) and from relationships estimated in our laboratory for Laurentian lakes (Comeau and Boisclair, unpublished). The size structure of the fish community at each sampling site was described by the percentage of fish belonging in each of the three size classes: SC_1; SC_2; SC_3.

Environmental characteristics

We estimated 15 environmental characteristics at each sampling site (Table 4.1). Average littoral slope (LS) was estimated as:

$$\mathrm{LS} = (z_2 - z_1) \times \Delta d_{2,1}^{-1} \quad (2)$$

where z_i is the depth at one location within a sampling site and Δd_i the difference of the distance between the two locations within the sampling site. The density of macrophytes at each site was estimated by two snorkellers in four randomly selected 1 m^2 quadrats (a 1 m^2 frame was thrown from the centre of the sampling site to different directions within each site). The number of stems from emergent and submersed species per 1 m^2 was counted. The average number of stems from the four replicates was used in the statistical analysis. The fetch was defined as the effective distance to the nearer shore in the direction of the predominant wind.

Table 4.1 Intrinsic and extrinsic (Spat) environmental variables that were respectively either sampled or computed at each sampling site for the sampling-site (S), the constant-multiple (C), or the habitat-patch (P) approaches. [1]: Percent of presence in all the sampling sites.

Variable	Code	Type	Approach	Resolution
Average littoral slope (m depth on 2 m)	LS	Intrinsic	S, C, P	Quantitative
Average depth (m)	Z	Intrinsic	S, C, P	Quantitative
Average temperature (°C)	Temp	Intrinsic	S, C, P	Quantitative
Average dissolved oxygen (mg L^{-1})	O_2	Intrinsic	S, C, P	Quantitative
<u>Substrates</u>				
Sand (< 2 mm)	S1	Intrinsic	S, C, P	P/A
Gravel (2 - 60 mm)	S2	Intrinsic	S, C, P	P/A
Rock (60 - 250 mm)	S3	Intrinsic	S, C, P	P/A
Boulder (> 250 mm)	S4	Intrinsic	S, C, P	P/A
Bedrock	S5	Intrinsic	S, C, P	P/A
Woody debris	S8	Intrinsic	S, C, P	P/A
<u>Macrophytes</u>				
Average density of emergent	Emer	Intrinsic	S, C, P	Quantitative
Average density of submersed	Sub	Intrinsic	S, C, P	Quantitative
Percent organic cover	Cov	Intrinsic	S, C, P	Percentage
Presence of pier	Pier	Intrinsic	S, C, P	P/A
Size	Size	Intrinsic	S, C, P	Quantitative
Type of patch	Hab	Intrinsic	P	Nominal
<u>Riparian use</u>				
Cabin/breakwater	U1	Extrinsic	S, C, P	P/A
Forest	U2	Extrinsic	S, C, P	P/A
Beach	U3	Extrinsic	S, C, P	P/A
Bush	U4	Extrinsic	S, C, P	P/A
Fetch (m)	Fet	Extrinsic	S, C, P	Quantitative
Distance to closest tributary (m)	Trib	Extrinsic	S, C, P	Quantitative
Distance to similar patch (m)	Dist	Extrinsic	P	Quantitative
Types of neighbour (east/west)	Neigh-E/W	Extrinsic	P	Nominal

Data analysis

Sampling-site approach.— Analyses conducted with the sampling-site approach were done using an analytical unit identical to the sampling site (Figure 4.2A). The relationships between the fish community descriptors and the environmental variables were estimated at the scale of individual sampling site.

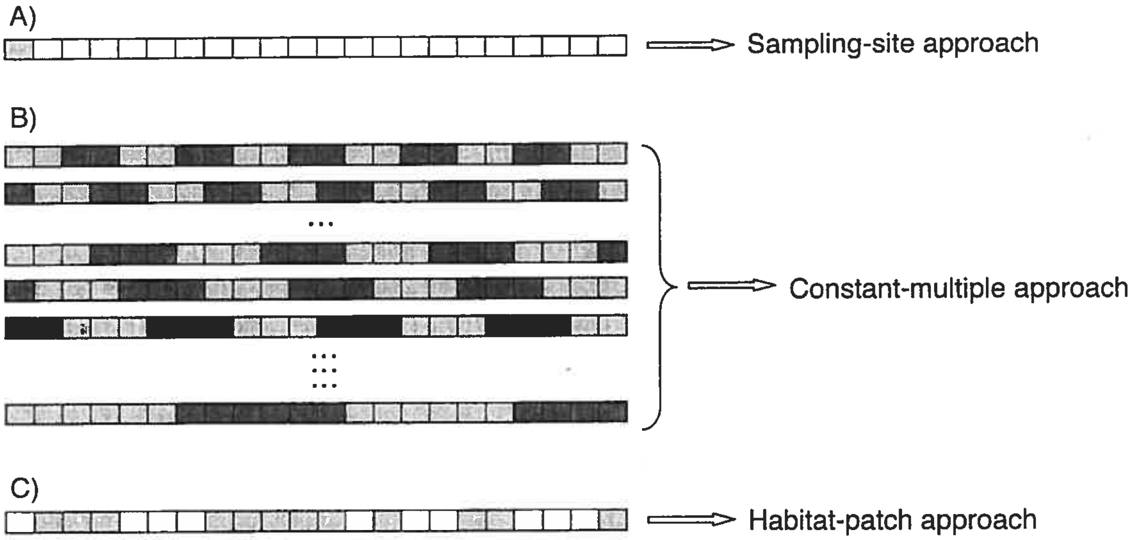

Figure 4.2 Schematic description of the three approaches used in this study, the sampling-site approach (A), the constant-multiple approach (B), and the habitat-patch approach (C).

Constant-multiple approach.— The constant-multiple approach consisted in the grouping of adjacent sampling sites (each having a surface area S) in units of increasing sizes (e.g. 2S or 3S, etc.; further referred to as groups of sites; Figure 4.2B). The analytical units in this approach are the groups of contiguous sampling sites. The analytical units could be viewed as a moving window of 1S, 2S, or 3S, etc. sampling units that shifts forward from any given arbitrary starting point around the lake to make all the possible combinations of merged sites. For instance, an analytical unit equal to 4S would have four different combinations of any given sampling site:

1) 1-2-3-4, 2) 2-3-4-5, 3) 3-4-5-6, or 4) 4-5-6-7. We never merged more than 6 sampling sites (6S). This limit was chosen because of statistical constraints. The grouping of six contiguous sampling sites lead to the formation of 15 analytical units of similar sizes. This number of analytical units was the minimum sample size that could be used in the statistical analyses, given the number of environmental predictors (Zar 1984). The sum of the values of the fish community descriptors (abundance, biomass, and size classes) were calculated in each analytical unit. Because the grouping of the sampling sites may induce an additive effect, we divided the values of each descriptor by the surface area (i.e. size) of their corresponding analytical unit. Environmental variables were averaged in each analytical unit.

Habitat-patch approach.— To verify the effect of habitat patches within the littoral zone, we classified the sampling sites into different types of habitat (Figure 4.2C). This was done using two complementary multivariate approaches: clustering and ordination. We identified clusters of sites defining different types of habitat using Ward's minimum variance analysis (WCA). This is a hierarchical clustering method that uses an objective function, the Sum of Squares (SS), the same criterion utilized in the multivariate analysis of variance. This method attempts to minimize the SS of any two (potential) clusters that can be formed (Legendre and Legendre 1998). Hierarchical methods are recommended when the variables to cluster are spatially and temporally dynamic (e.g. density of macrophytes). Visual confirmation of the clusters defined by WCA was obtained using a Principle Component Analysis (PCA; Legendre and Legendre 1998). Environmental variables were not dimensionally homogeneous (i.e. m, mg·L^{-1}, stems·m^{-2}, etc.), therefore the PCA was conducted on the correlation matrix, using R software (Legendre 2004). Following this procedure all contiguous sampling sites belonging to a same type of habitat were merged. Values of the fish community descriptors were summed in each habitat patch and we corrected for additive effect by dividing the descriptor values by the surface area of their corresponding patch. Environmental variables within each patch were also averaged. According to these calculations five new variables were generated: the type of habitat patch, the size of a habitat patch, the distance (in m) between two similar habitats, the type of neighbour on the east side, and the type of neighbour on the west side.

Intrinsic versus extrinsic environmental variables.— We assessed the impact of variables describing the spatial arrangement of analytical units by distinguishing two types of environmental variables: the intrinsic and the extrinsic variables (Table 4.1). We classified as intrinsic, the environmental variables that were estimated within an analytical unit. Intrinsic variables included the littoral slope, the average depth, the average temperature, the average dissolved oxygen, the type of substrate, the density of macrophytes, the presence of a pier, and the size of the analytical unit. Extrinsic variables were estimated using conditions found outside the analytical units. These variables included the riparian use, the fetch, and the distance to the closest tributary. However, some extrinsic variables were only estimated using the habitat approach. These variables were the one referring to the type of neighbouring habitat patch (east and west) and the smallest distance to a similar type of patch.

Fish habitat models.— We developed empirical models based on the relationships between fish community descriptors and environmental variables at the scale of the sampling sites (sampling-site approach), at the scale of a constant number of merged sampling sites (constant-multiple approach), and at the scale of the habitat patches (habitat-patch approach). In the constant-multiple approach, habitat models were developed for each combination of merged sampling sites. The number of models was equal to the number of combinations within each set of merged sites. For instance, for the analytical unit equal to 4S we developped four different models. The environmental variables were used as explanatory variables either in multiple regressions in the case of global metrics (total fish density, relative biomass, and size classes of the fish community), or in canonical redundancy analyses (RDA; Rao 1964) computed for the community composition (abundance of species) transformed using the Hellinger transformation as proposed by Legendre and Gallagher (2001). The RDA was computed for only two approaches: the sampling-site and the habitat-patch approaches. The identification of significant variables was done using either (1) a forward selection of the explanatory variables in SPSS (SPSS 1999) for the global metrics (single response variable), or (2) a forward selection procedure in the program CANOCO (ter Braak and Smilauer 1998) with unrestricted permutations for the community composition (multiple response variables). The threshold probabilities for the partial F statistics used in the selection were $p = 0.05$ to include a variable and $p = 0.10$ to remove a variable. Species present in less than 1% in the survey sites were excluded from all statistical analyses. We computed the R^2 as the fraction of the total variation of the response matrix accounted for by the explanatory data table, and corrected it using the adjusted R^2 formula (Zar 1984):

$$\text{Adjusted } R^2 = \quad 1 - [(1 - R^2) \times ((n-1)/(n-m-1))] \tag{3}$$

where *n* is the sample size and *m* is the number of independent explanatory variables.

We conducted an additional step in the development of habitat models using the habitat-patch approach. We verified if the predictive power obtained in models using patches based on environmental characteristics would be the same if the patches (same numbers and same sizes) were randomly distributed on the littoral zone of the lake. The verification was done by assessing and comparing the adjusted R^2 obtained at each of the 999 permutations that were performed in the previous analyses (multiple regression analyses and RDA) with the R^2 of the habitat-patch model.

RESULTS

The littoral zone of Lac Drouin showed considerable environmental variability across the sampling sites. The littoral slope (m depth on 2 m length) ranged from 0.00 to 1.19 m. The average depth within a sampling site ranged from 0.43 to 2.89 m. Average water temperature in the first 2.5 m depth ranged from 23.83 °C to 25.13 °C. Average dissolved oxygen in the first 2.5 m depth ranged from 5.98 mgL^{-1} to 6.64 mgL^{-1}. Rocks and woody debris were the most common types of substrate with a presence in over 40% of the sampling sites. These substrates were followed by sand and boulders with a presence in nearly 18% of the sites. Bedrock and gravel were the least common types of substrate with less than 1% of presence in the sampling sites. The average density of emergent macrophytes ranged from 0 to 86 stems m^{-2} while that of submersed macrophytes ranged from 0 to 19 stems m^{-2}. Nearly 2% of the sites had piers. The most common riparian uses were cabins and breakwaters (62% of the sites). The riparian zone consisted in forested areas in 47% of the sites. Bushes were present in 27% of the sites, and beaches in 6% of the sites. The fetch ranged from 0 to

1406 m. The distance between any given site and the closest tributary ranged from 0 to 1458 m. The average size of the sampling sites was 215 m^2 (range: 105 to 465 m^2).

Clustering of sampling sites

Grouping of the 90 sampling sites using WCA identified six clusters with two unclassified sites (Figure 4.3). These unclassified sites were considered outliers and were eliminated from further analyses. PCA ordinations of the site scores and environmental variables in three dimensions confirmed WCA solutions.

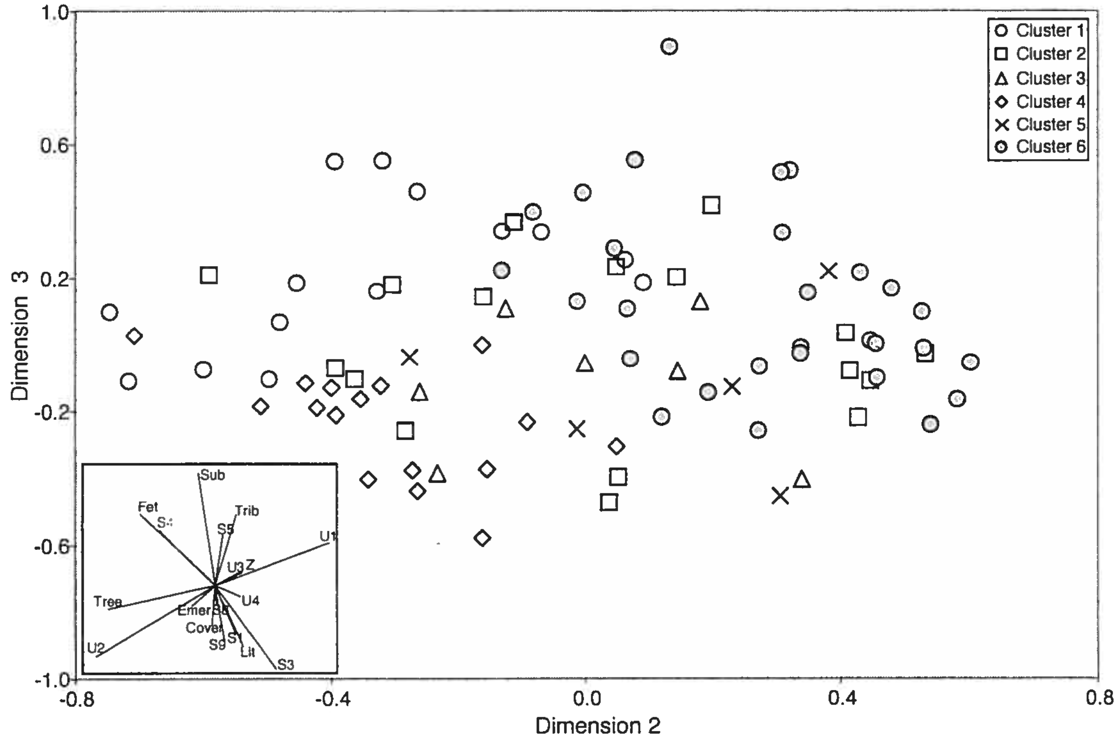

Figure 4.3 Sites scores on the second and third dimensions (12.6% and 8.7% of variance explained respectively) for the 90 sites located on the littoral zone of Lac Drouin. The symbols represent the six clusters identified by Ward's cluster analysis.

The first dimension of the PCA of the sampling sites accounted for 14.5% of the variance. The second and the third dimensions accounted for 12.6% and 8.7% respectively. Ordination of the second and third dimensions showed the most distinctive clusters. Clusters represented habitat types that differed mostly by their average depth, macrophyte density (emergent or submersed), fetch, the presence of woody debris and rocky substrates (Table 4.2).

Table 4.2 Environmental characteristics for each type of habitat display in the littoral zone of Lac Drouin.

Cluster no.	Main designation	Environmental characteristics
Cluster 1 (C1)	Exposed/rocky substrate	Exposed sites with an average fetch over 600 m where nearly 90% of the sites have boulders as substrate
Cluster 2 (C2)	Deep/low macrophyte density	Deep sites with an average over 1.85 m where 100% of the sites have a high riparian slope and poorly vegetated
Cluster 3 (C3)	Woody debris/forest/submersed	Sites with an important littoral slope where 100% of the sites have woody debris as substrate and where the average density of submersed macrophyte reaches 10 stems m^{-2}
Cluster 4 (C4)	Emergent/low slope	Sites with high density of emergent macrophyte (average: 12 stems m^{-2}), a medium fetch of 350 m and where 50% of the sites have sand as substrate
Cluster 5 (C5)	Protected/bush/emergent	Protected sites with an average fetch less than 20 m, with high density of emergent macrophyte (average: 12 stems m^{-2}) and surrounded by riparian bush
Cluster 6 (C6)	Cabins/deep/cover	Deep sites with an average over 1.85 m, where 90% of the sites have cabins on their riparian zone

These habitat types were spatially distributed in patches of various sizes representing a mosaic of habitats along the littoral zone of Lac Drouin (Figure 4.4).

The size of the patches ranged from 141 m^2 to 1175 m^2 but did not differ between habitat types (one-way ANOVA, $F_{5,38} = 1.507$, $p = 0.211$). This suggests that the six habitat types covered the same range of patch sizes. Over 80% of the littoral zone was covered by Clusters 6 (C6: 36.1%), 4 (C4: 25.9%), and 2 (C2: 18.6%). The other three clusters (C1: 11.2%; C3: 5.0%; C5: 3.2%) covered a total of nearly 20% of the littoral zone.

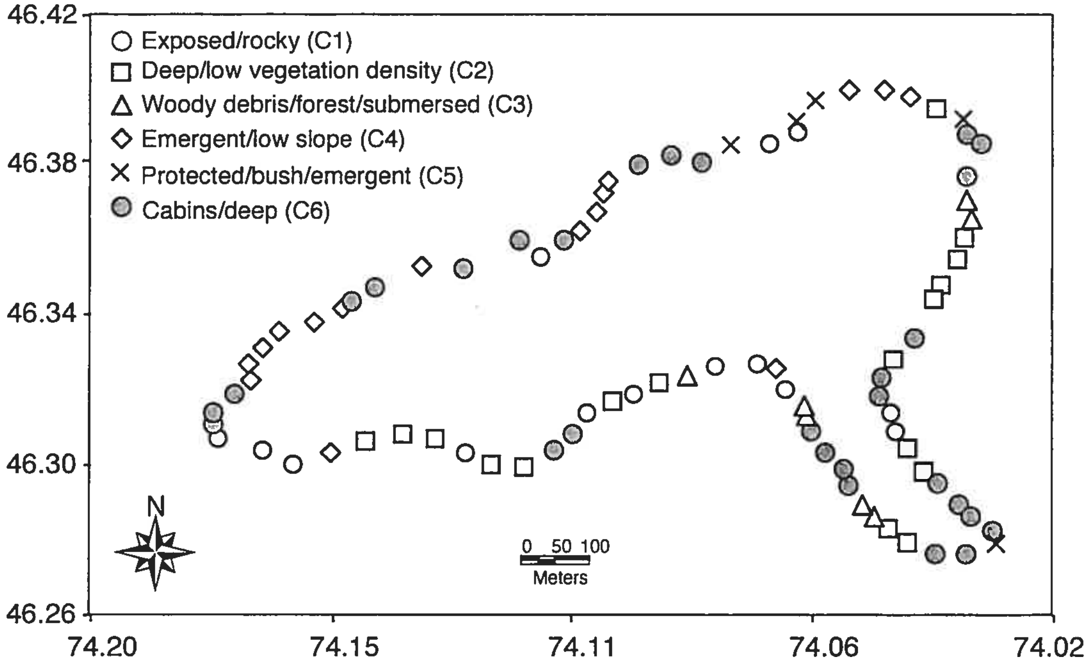

Figure 4.4 Spatial structure of the littoral zone of Lac Drouin. Codes for clusters are defined in Table 1.

Sampling-site approach

A total of 4293 fish belonging to eight species, were observed during the study. Pumpkinseed (*Lepomis gibbosus*) represented 51% of the fish observed. Six species represented less than 20% of the observations: golden shiner (*Notemigonus crysoleucas*), creek chub (*Semotilus atromaculatus*), banded killifish (*Fundulus* *diaphanus*), brown bullhead (*Ameiurus nebulosus*), yellow perch (*Perca flavescens*), and white sucker (*C. commersoni*). Fathead minnow (*Pimephales promelas*) represented less than 1% of fish observed.

The fish community descriptors varied greatly between sampling sites. The TFD ranged from 0.002 to 0.222 fish·m^{-2} (average = 0.078 fish·m^{-2}). Over 50% of the sampling sites had more than 0.065 fish·m^{-2}. The RB ranged from 0.016 to 5.262 g·m^{-2} (average = 0.938 g·m^{-2}) but only 30% of the sites had more than 1 g m^{-2}. SC$_1$ comprised 85% of the fish community whereas SC$_2$ and SC$_3$ represented respectively ~8% and ~7% of the fish community. SC$_1$ comprised at least 50% of the fish observed at any sampling site. No fish from SC$_2$ were observed in 30% of the sampling sites and these fish represented over 20% of the community in only 10% of the sites. Fish belonging to SC$_3$ were absent from more than 40% of the sites and represented more than 15% of the fish community in 20% of the sites.

Constant-multiple approach

Average values of the fish community descriptors were generally the same among the groups of analytical units (i.e. 1S, 2S, ... 6S; Table 4.3). One exception to this rule was the average TFD that varied between 0.235 fish·m^{-2} for the 1S group and 0.133 fish·m^{-2} for the other groups. However, average RB was relatively constant from 1S (2.814 g·m^{-2}) to 6S (2.690 g·m^{-2}). Similarly, the average percentage of SC$_1$ (84.56%), SC$_2$ (8.40%) and SC$_3$ (7.04%) varied by less than 1% between 1S and 6S.

Table 4.3 Summary of the variability of the community descriptors found for the constant-multiple approach among the six groupings of sampling sites.

Group	Descriptor	Minimum	Maximum	Mean
1S	TFD	0.002	0.222	0.078
	RB	0.016	5.262	0.937
	SC_1	50.000	100.000	84.560
	SC_2	0.000	35.090	8.390
	SC_3	0.000	34.290	7.040
2S	TFD	0.012	0.101	0.045
	RB	0.079	2.994	0.915
	SC_1	59.783	100.000	84.563
	SC_2	0.000	29.630	8.399
	SC_3	0.000	25.754	7.039
3S	TFD	0.014	0.097	0.045
	RB	0.105	2.375	0.907
	SC_1	62.944	100.000	84.562
	SC_2	0.000	27.566	8.399
	SC_3	0.000	23.650	7.039
4S	TFD	0.017	0.091	0.044
	RB	0.137	2.052	0.899
	SC_1	62.969	100.000	84.759
	SC_2	0.000	24.622	8.281
	SC_3	0.000	21.325	6.960
5S	TFD	0.020	0.082	0.044
	RB	0.204	1.861	0.899
	SC_1	65.158	99.231	84.562
	SC_2	0.000	22.660	8.399
	SC_3	0.000	20.949	7.039
6S	TFD	0.022	0.080	0.044
	RB	0.257	1.921	0.897
	SC_1	68.055	97.826	84.457
	SC_2	1.515	20.550	8.455
	SC_3	0.000	18.075	7.088

In contrast with the among-group variability, the within-group variability of the fish community descriptors reached between 5 to 13% (Table 4.3). The values of the fish community descriptors within groups of analytical units varied between 13 to 300-fold (the RB in the 1S unit).

Habitat-patch approach

Habitat patches showed great differences in fish community descriptors. For instance, the values of the TFD showed an 100-fold difference between habitat patches, reaching a maximum of 0.160 fish m^{-2} with an average of 0.073 fish$\cdot$$m^{-2}$. The RB ranged from 0.020 to 2.590 g$\cdot$$m^{-2}$ (average = 0.823 g$\cdot$$m^{-2}$). Percentage of fish belonging to SC_1 varied between 62 to 100%. SC_2 and SC_3 showed similar values, ranging from 0 to 25% and from 0 to 23% respectively.

Fish-habitat models

Sampling-site approach.— Fish habitat models developed with the sampling-site approach showed that the TFD and RB were correlated to the same environmental variables (Table 4.4). TFD and RB were correlated with the size of the sampling site, the fetch, and the dissolved oxygen. In addition, TFD was associated with the density of submersed macrophytes. These environmental variables explained from 20% (RB) and 31% (TFD) of the variability of fish descriptors. The percent contribution of the three fish size classes to the littoral community was explained by similar environmental variables (Table 4). The fetch ($\log_{10}$), the depth, and the dissolved oxygen explained a total of 25% of the among-site variability of the percentage of fish belonging to SC_1. Variation in the percentage of the fish community belonging to SC_2 was explained by the presence of boulders, the fetch, the presence of woody

Table 4.4 Sampling-site models developed for the total fish density (TFD). the relative biomass (RB) and the size classes of fish (SC_x) (n=90) and the relative contributions of the intrinsic and extrinsic variables. ***: $p \leq 0.001$.

Equation	Adjusted R^2	Intrinsic	Extrinsic
$TFD = 2.767 - 0.001\ Size - 0.133\ Log_{10}Fetch - 0.376\ O_2 + 0.006\ Sub$	0.31***	0.24	0.07
$RB = 53.261 - 0.014\ Size - 1.955\ Log_{10}Fetch - 7.628\ O_2$	0.21***	0.07	0.14
$SC_1 = -112.545 + 12.101\ Fetch - 5.246\ Depth + 32.787\ O_2$	0.25***	0.13	0.12
$SC_2 = 10.458 - 6.457\ S4 - 5.779\ Log_{10}Fetch + 3.854\ S8 - 11.927\ Pier$	0.25***	0.19	0.06
$SC_3 = 0.387 + 5.135\ Depth - 4.482\ Log_{10}Fetch$	0.19***	0.15	0.04

debris, and the presence of piers. These variables explained a total of 25% of the SC_2 variability. The fetch and the depth explained 19% of SC_3 variability.

Habitat models developed for the whole fish community using the redundancy analysis (RDA) showed that five environmental variables accounted for 58.1% of the among-site variability of the species composition. The ordination did not show obvious fish assemblages (Figure 4.5), but associations between the fish species and the environmental variables could be observed. *A. nebulosus* and *C. commersoni* were positively associated with the density of emergent macrophytes ($\log_{10}$).

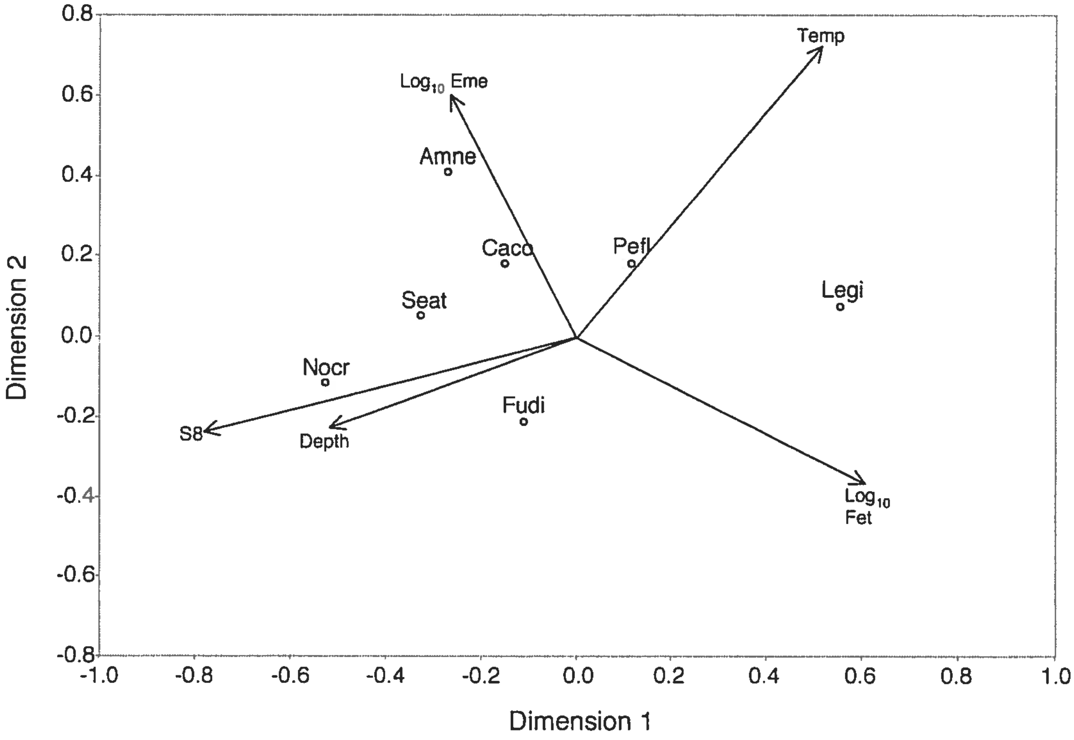

Figure 4.5 Ordination from the RDA showing the relationships between fish species and environmental variables for the habitat-patch model. Only the first dimension of each model was significant and accounted for 58.1% of the fish community variability.

The cyprinids (*N. crysoleucas* and *S. atromaculatus*) and *F. diaphanus* were positively associated with the presence of woody debris and the depth. *P. flavescens* were correlated with the temperature, whereas *L. gibbosus* showed no clear association with any environmental variable.

The relative contribution of intrinsic environmental variables (16%) was nearly twice as important as the contribution of the variables referring to spatial arrangement (9%) of the analytical unit (Fig. 6A and 6B). Two exceptions to this rule were the RB and the percentage of SC_1. The importance of intrinsic variables explained in the RB model (7%) were half less important than the extrinsic variables (14%), whereas both types of variables (intrinsic and extrinsic) showed equivalent relative contributions to the SC_1 model (~ 13%).

Constant-multiple approach.— The percentage of variance of the fish descriptors models explained by the environmental variables using the constant multiple-approach, varied widely within each group of analytical units (Table 4.5). For instance, in the 5S analytical unit the R^2 of the RB varied from 0.00 to 0.61. The environmental variables contributing most to the models also varied greatly among the groups analytical units (see details of models in Appendix A). However, certain associations between environmental variables and community descriptors gave consistently better R^2. The TFD variability in all the analytical units (1S to 6S) was best explained when either the size of the analytical unit or the presence of boulders was in the models (R^2 range: 0.31 to 0.84). The R^2 of the RB models were highest when the density of emergent macrophytes was included in the models (R^2 range: 0.66 to 0.90). The increase of R^2 in the RB models was particularly obvious in the 4S and 6S analytical units.

Table 4.5 Summary (mean R^2 and standard deviation; S.D.) of the constant-multiple models developed for the total fish density (TFD). the relative biomass (RB) and the size classes of fish (SC_x). *: Adjusted R^2.

Group	Descriptor	N	Mean R^{2*} (S.D.)
1S	TFD	1	0.31 (0.00)
	RB	1	0.20 (0.00)
	SC_1	1	0.25 (0.00)
	SC_2	1	0.25 (0.00)
	SC_3	1	0.19 (0.00)
2S	TFD	2	0.38 (0.06)
	RB	2	0.27 (0.09)
	SC_1	2	0.40 (0.07)
	SC_2	2	0.29 (0.11)
	SC_3	2	0.24 (0.20)
3S	TFD	3	0.43 (0.25)
	RB	3	0.29 (0.15)
	SC_1	3	0.50 (0.06)
	SC_2	3	0.44 (0.01)
	SC_3	3	0.32 (0.05)
4S	TFD	4	0.42 (0.14)
	RB	4	0.31 (0.28)
	SC_1	4	0.56 (0.11)
	SC_2	4	0.43 (0.43)
	SC_3	4	0.37 (0.21)
5S	TFD	5	0.55 (0.17)
	RB	5	0.28 (0.30)
	SC_1	5	0.65 (0.19)
	SC_2	5	0.47 (0.05)
	SC_3	5	0.35 (0.27)
6S	TFD	6	0.60 (0.18)
	RB	6	0.52 (0.30)
	SC_1	6	0.78 (0.12)
	SC_2	6	0.57 (0.31)
	SC_3	6	0.44 (0.16)

The models developed for the percentage of SC_1 showed higher R^2 in broader analytical units (4S to 6S), when the fetch and the presence of boulders were both in the models (R^2 range: 0.44 to 0.86). In the SC_2 models, the presence of boulders (negative correlation) was the variable contributing most to the R^2 in the 1S, 2S, and 3S analytical units (R^2 range: 0.22 to 0.44). At broader analytical units (4S to 6S), the presence of beaches together with the presence boulders (negative correlation), were the variables contributing the most in the SC_2 models (R^2 range: 0.45 to 0.89). In almost all the analytical units (1S to 5S), SC_3 variations were explained by models that comprised average depth as independent variable (R^2 range: 0.19 to 0.38). In the 6S analytical unit, variables related to the riparian use (forest, beach) were contributing most to the models. (R^2 range: 0.33 to 0.65).

Despite high variability observed within the groups of analytical units, the predictive power of models generally increased as the size of the analytical unit increased (average R^2, 1S: 0.24; 2S: 0.32; 3S: 0.40; 4S: 0.42; 5S: 0.46; 6S: 0.58). Significant differences in R^2 were found between the two smaller groups of analytical units (1S and 2S) and the larger group (6S; one-way ANOVA, $F_{5,99} = 4.863$, $p<0.001$).

The relative contribution of the intrinsic environmental variables to the models of the fish community descriptors was relatively stable across the sizes of the analytical units (Figure 4.6A). However, the relative contribution of the extrinsic variables increased with the size of the analytical units (Figure 4.6B). The later relationship was particularly strong for the three size classes of fish. Significant positive correlations were found between the relative contribution of extrinsic variables and the size of analytical units (SC1: Pearson r = 0.60, n = 21, p = 0.004; SC2: Pearson r = 0.67, n = 21, p = 0.001; SC3: Pearson r = 0.50, n = 21, p = 0.021).

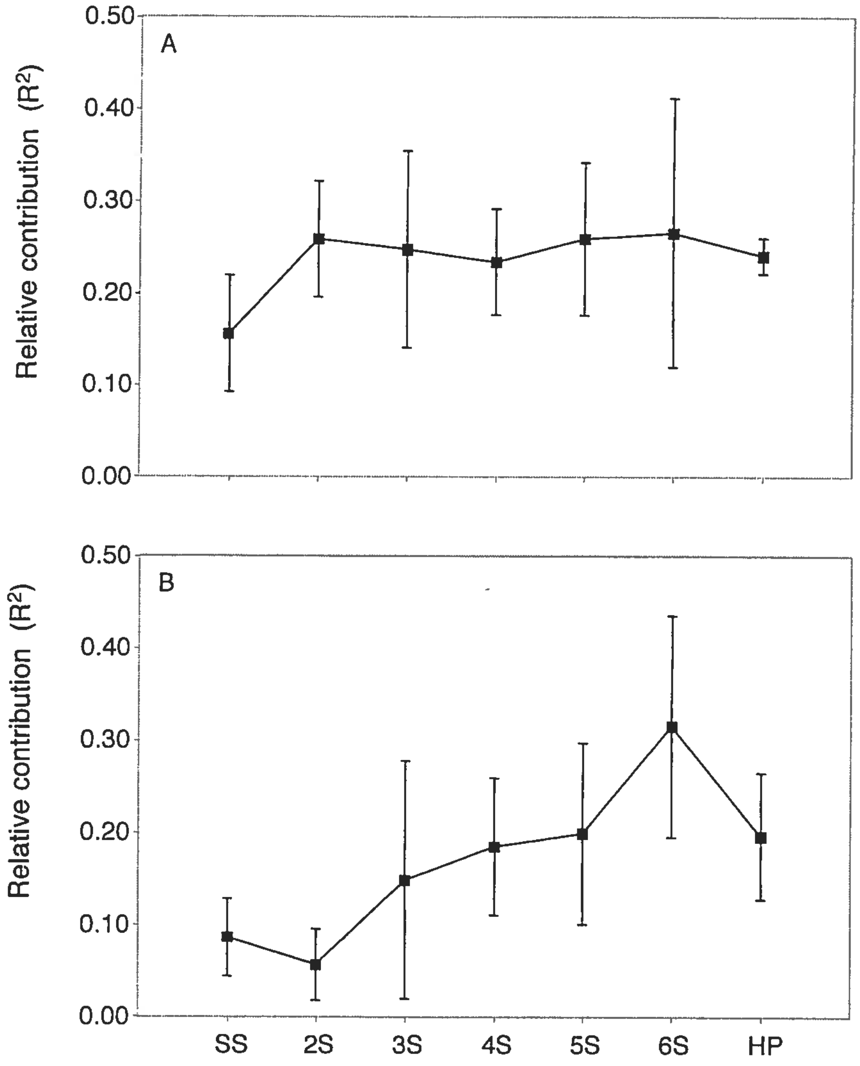

Figure 4.6 Relative contributions of the local variables (A) and the spatial arrangement variables (B) to the three types of models

Habitat-patch approach.— Predictive power (R^2) of the models developed using the habitat-patch approach ranged from 0.37 (SC_3) to 0.53 (SC_1) (Table 4.6).

Table 4.6 Habitat-patch empirical models developed for the total fish density (TFD). the relative biomass (RB) and the size classes of fish (SC_x). Variable codes are defined in Table 1. ***: $p \leq 0.001$.

Equation	Adjusted R^2	Intrinsic	Extrinsic
$TFD = 0.079 + 0.030\ S8 - 0.026\ Log_{10}Fet - 0.018\ U2$	0.45***	0.26	0.19
$RB = 0.834 - 0.923\ Log_{10}Fet + 0.820\ Log_{10}Sub$	0.44***	0.25	0.19
$SC_1 = 123.570 + 17.702\ Log_{10}Fet - 0.014 - 15.992\ Log_{10}Size - 10.665\ Log_{10}Sub$	0.53***	0.22	0.31
$SC_2 = 12.977 - 6.508\ S4 - 6.517\ Log_{10}Fetch$	0.39***	0.26	0.14
$SC_3 = -16.334 - 8.806\ Log_{10}Fetch + 7.346\ Log_{10}Sub + 9.032\ Log_{10}Size$	0.37***	0.22	0.15

Fetch was an important predictor of the fish community descriptors explaining 13 to 31% of the total variability in every model. The presence of woody debris, the fetch, and the presence of forest on the riparian shore explained 45% of the TFD variability. Model developed for the RB included two variables, the fetch and the density of submersed macrophytes. Together the two variables explained 44% of the RB variability. The fetch and the size of the habitat patch were the two variables explaining 53% of the SC_1 variability. Model developed for the SC_2 included the fetch and the presence of boulders. The two variables explained 39% of the SC_2 variability. Environmental variables contributing to the SC_3 model accounted for 37% its among-patch variability. The fetch and the size of habitat patches were the two variables correlated with SC_3.

Redundancy analysis performed on the fish community composition showed the presence of two main fish assemblages, each influenced by dominant environmental variables (Figure 4.7). Only the first dimension was statistically significant and accounted for 64.5% of the fish community variability. The first assemblage was represented by *S. atromaculatus* and *N. crysoleucas* and was correlated with the presence of woody debris and sand. The two species were three (*S. atromaculatus*) and six times (*N. crysoleucas*) more abundant in patches with woody debris than in patches without this substrate (one-way MANOVA, $F_{2,41} = 6.636$, $p < 0.003$). The second assemblage was characterized by *P. flavescens*, *C. commersoni*, and *A. nebulosus*. These species were associated with the types of habitat and the types of neighbouring patches. They displayed higher densities in deep habitat patches and in highly vegetated patches with emergent macrophytes.

Lower densities were found in habitat patches with high fetch values and with woody debris as substrates. The three species also displayed high densities when the neighbouring patches were highly vegetated with medium fetch values (~ 250 m).

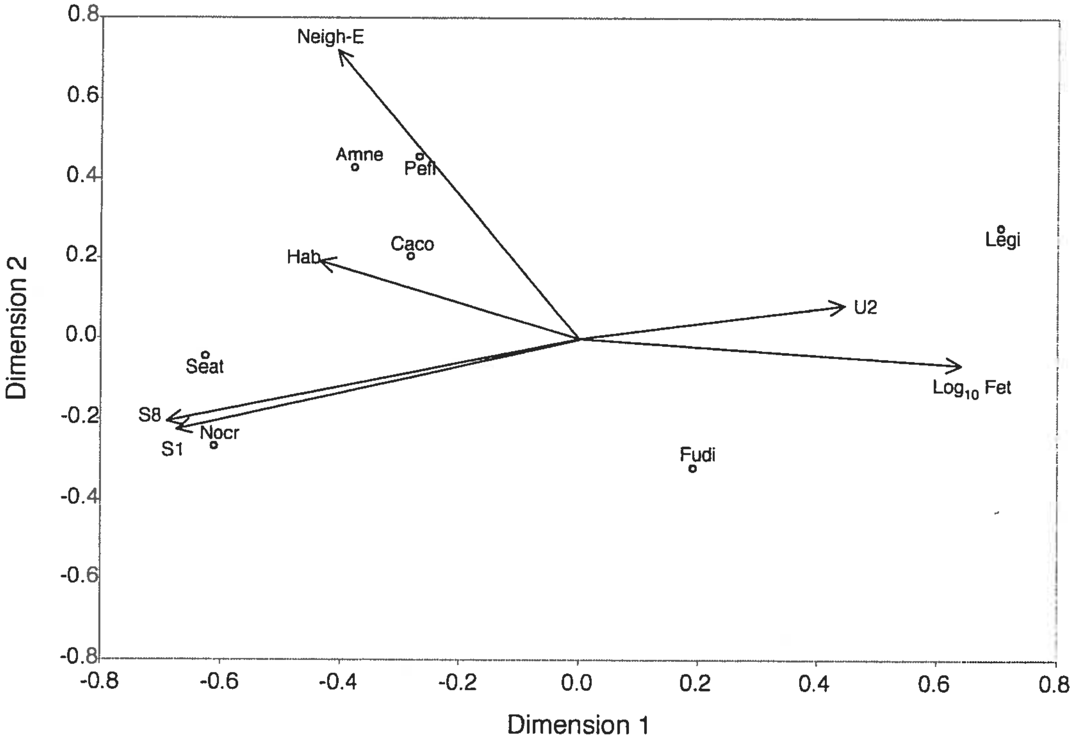

Figure 4.7 Ordination from the RDA showing the relationships between fish species and environmental variables for the sampling-site approach. Only the first dimension was significant and accounted 64.5% of the fish community variability.

Highly exposed patches as neighbours had a negative impact on *P. flavescens*, *C. commersoni*, and *A. nebulosus* densities. *L. gibbosus* and *F. diaphanus* displayed two distinct single species associations with the environmental variables. *L. gibbosus* were correlated with the fetch ($\log_{10}$) and the presence of forest. *F. diaphanus* were correlated with the types of neighbouring patches. High densities of *F. diaphanus* were found when the neighbouring patches were composed of woody debris. When the neighbouring patches were characterized by high average depth and cabins on their riparian shore, the *F. diaphanus* showed lower densities.

The relative contribution of the intrinsic variables was relatively stable among the models, representing between 22 to 27% of the total variability of the fish community descriptors (Table 4.6). The extrinsic variables showed more variability, contributing for 14 to 37% of the total variability of the fish community descriptors. Among the extrinsic variables, the fetch (R^2: 0.05 to 0.31) and the type of neighbour on the east side (R^2: 0.13) were the two most contributing variables.

Randomly distributed patches.— Models obtained using habitat-patch approach defined by environmental characteristics displayed R^2 that were 5 to 10-fold higher than models obtained by randomly distributed patches in the littoral zone of Lac Drouin (Table 4.7). Predictive power of the models developed with the environmental-defined patches always ranked in the first percentile of the permuted R^2 distributions. These results suggest that the environmental composition and the spatial arrangement of habitat patches are significantly influencing the fish community of Lac Drouin.

Table 4.7 Summary (R^2, standard deviation; S.D., percentile; perc, minimum; min, and maximum; max) of the habitat-patch models using obtained by habitat patches randomly distributed in the littoral zone of the lake. R^2 for the habitat-patch models obtained with patches based on environmental characteristics are found in Table 4.6.

Random	TFD	RB	SC_1	SC_2	SC_3	Abundance
Mean R^2	0.066	0.043	0.067	0.069	0.069	0.139
S.D.	0.052	0.040	0.048	0.039	0.051	0.039
Perc	1st	1st	1st	1st	1st	1st
Min	0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.051
Max	0.346	0.245	0.286	0.345	0.263	0.325

DISCUSSION

Several studies have shown that littoral zones of lakes consist in a mosaic of habitat patches (Eadie and Keast 1984, Benson and Magnuson 1992, Chick and McIvor 1994, Weaver et al. 1997, Brosse et al. 1999, Grenouillet and Pont 2001). However, very few of them have tested the effect of the size of analytical units to study fish-habitat relationships, despite the evidence that patches may play an important role as functional units for different fish species and size classes (Weaver et al. 1997, Kocik and Ferreri 1998). Our study tested the effect of three approaches on the predictive power of fish habitat models. The use of the constant-multiple and the habitat-patch approaches instead of the sampling-site approach increased the predictive power of the habitat models from an average of 24% of the fish community variability (sampling-site approach) to 40% (average of constant-multiple approach) and 44% (habitat-patch approach). Our study also showed that the nature of the variables explaining attributes of littoral fish communities changed with the size of the analytical units. The relative contribution of the extrinsic variables increased with the size of the analytical units. On average, the extrinsic variables represented 9%, 18%, and 20% of the total variability in the sampling-site, constant-multiple approach, and habitat-patch approach models respectively.

Size of analytical units

Predictive power of fish-habitat models may be highly influenced by the merging of sampling sites, often because biological processes may occur at spatial scales broader than the sampling scale at which the study is performed (Cooper et al. 1998). For instance, the dispersal capability of a species may encompass several sampling units even within a specific period of a day (dawn, day, dusk). Consequently, the fish densities collected at the scale of the sampling site may be low and highly variable (Cooper et al. 1998). In such case, the clustering of sampling sites may average out the intrinsic variability and produce more robust predictive relationships between the fish and their environment (Poff 1997). Predictions made by geostatistical studies on the effect of changing the size of the analytical units on the variance of aggregated units state that the variance of the aggregated samples should decrease linearly with the number of sampling units in an aggregated sample. As the size of the analytical units increases, the range of autocorrelation increases, while the variance and the proportion of noise in the data decrease (Bellehumeur and Legendre 1997). These predictions were partly supported by our results for which increasing R^2 were observed with the increase of the size of the analytical units. However, if our results were solely explained by the geostatistical phenomenon the constant-multiple approach would have given systematically highest R^2 for every model developed within the largest analytical units. This was not the case and the coefficients of variation of the models developed using the constant-multiple approach were highly variable ranging from 0% to 107% with an average of 34.7%. We suggest that the high variability observed in the constant-multiple models may also be explained by the environmental characteristics on which the analytical units were based. For instance, a random merging of sampling sites may have no ecological relevance and therefore no consistent impact on the predictive power of the models. The merging of sites that occasionally resulted in the combination of similar contiguous habitats likely increased the R^2 of these models.

Concurrently, since predictive power of fish-habitat models is influenced by the sample size and the number predictive variables used in the model, we computed adjusted R^2 which accounts for the variability of the two parameters. We also conducted bootstrap analyses on all the sizes of analytical units using the same sample size (n=12). Results from these two analyses were highly correlated (Pearson $r = 0.68$, $df = 13$, $p = 0.005$) and confirmed that the observed increase in R^2 with the size of the analytical units was not a statistical artifact.

Why use habitat patches?

Littoral zones of lakes are known to display a diversity of micro-habitats composed of a variety of physical and biological structures, such as rocky substrates and macrophyte beds (Werner et al. 1977, Chick and McIvor 1994). As opposed to a random process such as the constant-multiple approach, the merging of the sites using the habitat-patch approach presumably matched the spatial structure of the heterogeneous environment of the littoral zone of Lac Drouin. We may argue that by using the clustering of contiguous sampling sites in patches of different sizes, the habitat-patch approach incorporated functional information on different habitat requirements of fish species. For instance, considering multiple spatial scales, Brind'Amour et al. (submitted) recently showed the influence of the interaction between the spatial context and the environment (i.e. habitat characteristics) on the functional organization of littoral fish communities. They suggested the presence of functional relationships between fish species and their habitat, principally established on the criteria of where and how resources are used by species within the water column.

The greatest predictive power obtained with the models developed using habitat patches based on environmental characteristics in comparison to the models developed using randomly distributed habitat patches, underlines the importance of the spatial arrangement of habitat patches in structuring littoral fish communities. This result also suggests that an arbitrarily definition of conservation units would not be effective as a definition of conservation units based on ecological information. This is particularly interesting in a management perspective, where conservation programs often use global target such as percent of total surface area to be protected, our study emphasizes the importance of relating this percentage to environmental features located inside and outside the habitat.

Influence of the extrinsic variables

The sampling of environmental variables outside the sampling sites and the clustering of the sampling sites into habitat patches, allowed us to create extrinsic variables that are rarely included in fish habitat models (Hanchin and Willis 2003).

The relative contribution of these extrinsic variables was on average twice as high for the habitat models developed using the habitat-patch approach in comparison to the sampling-site approach. Although these spatial variables were mostly important in the habitat-patch approach, significant proportions of the explained variability using the sampling-sites approach were also related to the extrinsic variables (range : 4% to 14% of the total variability explained). This suggests that the commonly developed habitat models, using intrinsic variables, would benefit from the inclusion of spatially structured variables measured outside the sampling site such as the fetch, distance to tributaries, and riparian use.

The greatest difference between the constant multiple and the habitat patch approaches was observed in the species composition (i.e. RDA analyses). Using the habitat patch approach, the extrinsic variables accounted for nearly 60% of the total variance of the species composition whereas these variables represented only 20% of the total variance of the species composition using the sampling-site approach. The type of habitat and the type of neighbour were the two most important variables differencing the two approaches. Our results showed that habitat patches displaying similar intrinsic environmental characteristics might differ in their species composition and fish density depending on the type of environmental characteristics of the surrounding patches (or neighbours; Bohnsack 1991). Our study corroborates the results of Weaver et al. (1997) who found that the integration of variables describing the spatial arrangement of habitat within the littoral zone of the lake likely enhanced the understanding of fish-habitat relationships.

Size-structured patchiness

The size of the habitat patch was an important predictor of the fish-habitat models and principally in the models developed for the size structure of the fish community. The density of small fish was lowest in large patches whereas the opposite trend was observed for large fish. It may be argued that fish density, irrespective of the size class, would increase with the size of the patches. Habitats distributed in larger patches may display wider range of environmental conditions in comparison to smaller patches and thus decrease inter-specific competition thereby supporting greater densities of fish (Dunham et al. 2001). However, our results did not support this expectation. We may argue that the size of an habitat patch is organism-dependent (Wu and Loucks 1995). For instance, an habitat patch of 150 m^2 could be perceived either as small or large depending on the size of the fish that occupies it. In our study, the minimum size that could be reached by the small-sized class (30 mm) was 10 times smaller than the maximum size that could be reached by the large-sized class (320 mm). Further, differences in the utilization of the size of an habitat between the small and large-sized classes might be the results of scale-dependent responses (Wiens 2002). Small-sized fish species may respond to fine scale habitat variation whereas large-sized species responded to habitat variation at broader spatial scale. The spatial succession of small structurally complex patches, such as those observed in our study, may be more appealing to small fish than larger patches because small patches provide both shelter and higher densities of cladocerans in association to open spaces and edges (small patches = higher edge/surface ratio; Nurminen and Horppila 2002).

Along with the size of habitat patches, the fetch and the density of submersed macrophytes influenced differently the smallest and the largest size classes of the fish community. Small-sized fish were associated with exposed patches with low density of submersed macrophytes but large-sized fish were correlated with protected patches with high density of submersed macrophytes. Keddy (1983) demonstrated that intermediate fetch values may be beneficial to macrophytes growth and that species composition of macrophytes beds may vary between exposed and protected shores. Although we did not distinguish macrophytes species, it is possible that both the exposed and protected shores differed in their macrophytes composition and offered different habitat quality to the two size classes of fish (Grenouillet and Pont 2001). The linear relationship between the size of the fish and the fetch seemed in contradiction with the findings of Randall et al. (1996), who observed a non-linear relationship between the fetch and the size of the fish. However, their study was conducted in small bays of Lake Ontario where the fetch reached values three times larger than in Lake Drouin. When similar fetch values were compared, both studies observed a negative relationship between the size of the fish and the fetch. Larger fish were most abundant in low fetch values whereas smaller fish were most abundant in high fetch values. These results suggest that fetch likely affected indirectly the fish community of Lac Drouin, either by its involvement in the determination of benthic production (Burkholder 1992, Cyr 1998) or by its participation in the structuring of littoral habitats (e.g. macrophyte beds; Keddy 1983).

Conclusion and perspective

Over the past decades the emerging discipline of landscape ecology has been focusing on the influence of spatial patterns on ecological processes and notably on the effect of patchiness on biological communities (Wiens et al. 1993). Wiens (2002) recently stated that "the principles and approaches of landscape ecology can be extended to include freshwater systems", referring to river ecosystems. As littoral zones of lakes are often described as a landscape composed of multiple habitat layers of various sizes and qualities (Chick and McIvor 1994, Brind'Amour et al. 2005), landscape ecology could also offer important insights in the study of fish-habitat relationships in lakes. Our study showed that by integrating the 'landscape context' (i.e. spatial arrangement of habitats) in the development of fish-habitat models, we significantly enhanced our understanding of fish-habitat relationships in the littoral zone of the studied lake. Furthermore, we provided a quantitative support to the idea that the spatial attribution of conservation units within a lake should be defined based on environmental characteristics rather than defined randomly.

APPENDIX A

Empirical models developed using the constant-multiple approach for the total fish density (TFD). the relative biomass (RB) and the size classes of fish (SC_x). Variable codes are defined in Table 1. ***: $p \leq 0.001$.

	Equation	Adjusted R^2	Intrinsic	Spatial
1S	$TFD = 2.767 - 0.001\ Size - 0.133\ Log_{10}Fetch - 0.376\ O_2 + 0.006\ Sub$	0.31***	0.10	0.21
	$RB = 53.261 - 0.014\ Size - 1.955\ Log_{10}Fetch - 7.628\ O_2$	0.20***	0.07	0.13
	$SC_1 = -112.545 + 12.101\ Fetch - 5.246\ Depth + 32.787\ O_2$	0.25***	0.13	0.12
	$SC_2 = 10.458 - 6.457\ S4 - 5.779\ Log_{10}Fetch + 3.854\ S8 - 11.927\ Pier$	0.25***	0.19	0.06
	$SC_3 = 0.387 + 5.135\ Depth - 4.482\ Log_{10}Fetch$	0.19***	0.15	0.04
2S	$TFD = 0.249 - 2.947E^{-4}\ Size + 0.038\ S8 - 0.036\ S4$	0.33***	0.18	0.15
	$RB = -1.579 + 1.928\ Depth + 1.492\ Log_{10}\ Emer$	0.21***	0.21	0.00
	$SC_1 = 89.730 - 8.500\ Depth + 7.826\ S4 + 0.008\ Trib + 6.084\ U4$	0.45***	0.33	0.12
	$SC_2 = 13.384 - 6.403\ S4 - 0.005\ Trib$	0.22***	0.15	0.07
	$SC_3 = -6.076 + 7.921\ Depth$	0.25***	0.25	0.00
2S	$TFD = 0.244 - 3.239E^{-4}\ Size - 0.047\ S4 + 0.030\ S8 + 0.031\ U1$	0.42***	0.21	0.21
	$RB = 6.745 - 1.740\ S4 - 0.011\ Size + 1.455\ U1$	0.33***	0.14	0.19

	$SC_1 = 77.935 + 9.457\ S4 + 9.847\ \mathrm{Log}_{10}\mathrm{Fetch}$	0.35***	0.24	0.11
	$SC_2 = 8.661 - 5.226\ S4 + 5.831\ \mathrm{Log}_{10}\mathrm{Emer} - 0.005\ \mathrm{Trib}$	0.37***	0.28	0.09
	$SC_3 = 0.225 + 5.332\ \mathrm{Depth} - 4.831\ \mathrm{Log}_{10}\mathrm{Fetch}$	0.22***	0.16	0.04
3S	$TFD = 0.327 - 3.291E^{-4}\ \mathrm{Size} - 0.047\ S4 + 0.051\ U3 + 0.122\ \mathrm{Litt}$	0.61***	0.18	0.43
	$RB = 8.115 - 0.008\ \mathrm{Size} - 2.275\ \mathrm{Log}_{10}\mathrm{Fetch} + 0.183\ \mathrm{Sub}$	0.42***	0.10	0.31
	$SC_1 = 74.877 + 8.737\ \mathrm{Log}_{10}\mathrm{Fetch} + 8.517\ S4 + 6.370\ U4$	0.50***	0.14	0.36
	$SC_2 = 28.660 - 5.842\ S4 - 0.025\ \mathrm{Size} - 5.585\ \mathrm{Log}_{10}\mathrm{Fetch}$	0.43***	0.22	0.21
	$SC_3 = -5.848 + 9.386\ \mathrm{Depth} - 3.982\ S8$	0.33***	0.33	0.00
3S	$TFD = 0.110 + 0.050\ S8 - 0.040\ S4 - 1.751E^{-4}\ \mathrm{Size}$	0.53***	0.43	0.10
	$RB = 2.248 - 1.517\ S4 + 1.282\ S8$	0.33***	0.33	0.00
	$SC_1 = 74.558 + 10.197\ \mathrm{Log}_{10}\mathrm{Fetch} + 7.770\ U4 + 7.869\ S4$	0.56***	0.12	0.44
	$SC_2 = 211.699 - 5.262\ S4 - 0.006\ \mathrm{Trib} - 32.392\ O_2$	0.44***	0.35	0.09
	$SC_3 = -6.802 + 8.359\ \mathrm{Depth}$	0.27***	0.27	0.00
3S	$TFD = 0.151 - 0.045\ S4$	0.14***	0.14	0.00
	$RB = 3.280 - 1.410\ S4$	0.12***	0.12	0.00
	$SC_1 = 83.965 + 12.076\ \mathrm{Log}_{10}\mathrm{Fetch} + 10.020\ U4 - 12.679\ \mathrm{Log}_{10}\mathrm{Emer}$	0.44***	0.14	0.30
	$SC_2 = 3.874 + 11.836\ \mathrm{Log}_{10}\mathrm{Emer} - 6.132\ \mathrm{Log}_{10}\mathrm{Fetch} - 3.852\ U4$	0.44***	0.23	0.21
	$SC_3 = 12.715 - 5.995\ U4 - 5.934\ \mathrm{Log}_{10}\mathrm{Fetch}$	0.37***	0.00	0.37
4S	$TFD = 2.446 - 0.379\ O_2 + 0.050\ U3$	0.33***	0.190	0.14
	n.s.			

	$SC_1 = 88.556 + 13.063\ \mathrm{Log_{10}Fetch} + 7.768\ S4 + 11.337\ S9 - 7.585\ \mathrm{Depth}$	0.69***	0.37	0.32
	$SC_2 = 9.232 - 5.687\ S4 + 5.645\ U3$	0.46***	0.30	0.16
	$SC_3 = -8.976 + 9.740\ \mathrm{Depth}$	0.37***	0.37	0.00
4S	$TFD = 0.257 - 0.060\ S4 - 1.652E^{4} + 0.053\ U1$	0.53***	0.27	0.26
	$RB = 1.685 - 2.165\ S4 + 2.308\ U1$	0.38***	0.19	0.19
	$SC_1 = 71.844 + 9.634\ S4 + 10.731\ U2$	0.60***	0.39	0.21
	$SC_2 = 9.449 - 5.813\ S4 + 7.112\ U3$	0.45***	0.22	0.23
	$SC_3 = 15.858 - 8.513\ U2 - 4.390\ S4$	0.67***	0.17	0.50
4S	$TFD = 0.097 + 0.053\ S8$	0.28***	0.280	0.00
	$RB = 3.398 - 1.784\ U4 + 1.803\ \mathrm{Log_{10}Emer} - 0.001\ \mathrm{Trib} - 0.977\ S4$	0.66***	0.26	0.40
	$SC_1 = 71.293 + 10.556\ U4 + 7.607\ S4 + 0.009\ \mathrm{Trib}$	0.51***	0.11	0.40
	$SC_2 = 4.463 - 7.178\ U4 + 9.580\ \mathrm{Log_{10}Emer}$	0.37***	0.18	0.19
	$SC_3 = 9.615 - 5.435\ U4$	0.20***	0.00	0.20
4S	$TFD = 0.103 + 0.045\ S8 + 0.045\ U3 - 0.036\ S4$	0.55***	0.35	0.20
	$RB = 3.244 - 1.489\ S4$	0.19***	0.19	0.00
	$SC_1 = 77.447 + 10.351\ \mathrm{Log_{10}Fetch} + 8.032\ S4$	0.44***	0.14	0.30
	$SC_2 = 9.377 - 6.053\ S4 + 6.367\ U3$	0.46***	0.29	0.17
	$SC_3 = -7.511 + 8.774\ \mathrm{Depth}$	0.25***	0.25	0.004
5S	$TFD = 0.177 - 0.048\ S4 - 0.042\ U4$	0.43***	0.22	0.21
	$RB = 4.448 - 1.867\ U4 - 1.537\ S4$	0.59***	0.27	0.32

	$SC_1 = 77.336 + 11.054\ Log_{10}Fetch - 11.960\ Log_{10}Emer + 7.894\ U4 + 6.344\ U2 + 5.238\ S4$	0.85***	0.24	0.61
	$SC_2 = 9.519 - 6.246\ S4 + 5.889\ U3$	0.47***	0.19	0.06
	$SC_3 = 7.896 + 4.090\ Depth - 4.894\ Log_{10}Fetch - 3.788\ U4 - 3.891\ U2$	0.76***	0.46	0.30
5S	$TFD = 2.389 - 0.365\ O_2 - 4.017E^{-5}\ Trib$	0.22***	0.22	0.00
	$RB = 9.152 - 0.006\ Size$	0.19***	0.00	0.19
	$SC_1 = 46.118 + 10.606\ U2 + 9.642\ Log_{10}Fetch + 5.508\ S4 - 0.021\ Size$	0.80***	0.09	0.71
	$SC_2 = 8.782 + 8.026\ U3 - 3.871\ S4$	0.50***	0.12	0.38
	$SC_3 = 14.633 - 8.544\ U2$	0.31***	0.00	0.31
5S	$TFD = 0.268 - 1.658E^{-4}\ Size - 0.035\ S4 + 0.177\ Litt + 0.046\ U3$	0.72***	0.31	0.42
	RB = n.s.			
	$SC_1 = 74.712 + 12.925\ Log_{10}Fetch + 6.514\ S4 + 10.216\ S9$	0.70***	0.35	0.35
	$SC_2 = 8.907 + 7.489\ U3 - 4.345\ S4$	0.52***	0.17	0.35
	SC_3 = n.s.			
5S	$TFD = 0.101 - 0.042\ S4 + 0.060\ U3 + 0.047\ S8$	0.73***	0.44	0.29
	RB = n.s.			
	$SC_1 = 76.307 + 10.610\ Log_{10}Fetch + 7.449\ S4$	0.44***	0.18	0.26
	$SC_2 = 8.971 + 7.027\ U3 - 4.268\ S4$	0.45***	0.15	0.30
	$SC_3 = -9.793 + 10.166\ Depth$	0.28***	0.28	0.00
5S	$TFD = 0.158 - 0.059\ S4$	0.48***	0.48	0.00

	$RB = 1.724 - 2.878\ U4 + 3.553\ Log_{10}Emer$	0.61***	0.35	0.26
	$SC_1 = 99.937 + 10.331\ S4 - 12.058\ Depth$	0.48***	0.48	0.00
	$SC_2 = 11.624 - 7.257\ S4$	0.38***	0.38	0.00
	$SC_3 = -11.218 + 11.026\ Depth$	0.38***	0.38	0.00
6S	$TFD = 2.844 - 0.046\ S4 - 0.435\ O_2 - 5.442E^{-5}\ Trib$	0.84***	0.70	0.14
	$RB = 4.663 - 1.608\ S4 - 1.623\ U4$	0.48***	0.24	024
	$SC_1 = 65.243 + 10.961\ S4 + 12.312\ U2 + 0.007\ Trib$	0.85***	0.34	0.51
	$SC_2 = 23.612 - 6.482\ S4 + 3.631\ U3 - 5.155\ Log_{10}Fetch - 0.008\ Size$	0.88***	0.49	0.39
	$SC_3 = 15.010 - 9.198\ U2$	0.33***	0.00	0.33
6S	$TFD = 1.871 - 0.034\ S4 + 0.040\ U3 - 0.283\ O_2$	0.73***	0.50	0.23
	RB = n.s.			
	$SC_1 = 67.067 + 11.724\ U2 + 8.816\ S4 + 7.521\ Log_{10}Fetch$	0.81***	0.37	0.44
	$SC_2 = 13.117 + 6.458\ U3 - 4.405\ S4 - 4.563\ U2$	0.75***	0.19	0.56
	$SC_3 = -5.836 + 7.775\ Depth$	0.22***	0.22	0.00
6S	$TFD = 2.960 - 0.464\ O_2 + 0.046\ U3$	0.57***	0.35	0.22
	$RB = 0.965 - 2.835\ U4 + 3.616\ Log_{10}Emer + 0.947\ S8$	0.90***	0.49	0.41
	$SC_1 = 88.149 + 19.116\ U3 - 18.773\ Log_{10}Emer - 4.116\ S1$	0.88***	0.44	0.44
	$SC_2 = 6.783 - 6.060\ U3$	0.26***	0.00	0.26
	$SC_3 = 13.463 - 8.760\ U4$	0.65***	0.00	0.65
6S	$TFD = 0.150 + 0.047\ U3 - 0.042\ U4$	0.46***	0.00	0.46

	RB = 2.139 – 2.394 U4 + 2.816 Log_{10}Emer	0.68***	0.36	0.33
	SC_1 = – 26.732 + 28.410 Log_{10}Fetch + 0.084 Size – 0.019 Trib	0.70***	0.00	0.70
	SC_2= 6.794 + 6.019 U3	0.27***	0.00	0.27
	SC_3 = 12.036 – 6.814 U4	0.47***	0.00	0.47
6S	TFD = 0.153 – 0.045 S4	0.37***	0.37	0.00
	RB = 4.052 – 1.382 S4 – 1.083 U4	0.49***	0.33	0.16
	SC_1 = 44.005 + 14.641 Log_{10}Fetch – 0.026 Size	0.57***	0.00	0.57
	SC_2= 6.612 + 6.754 U3	0.34***	0.00	0.34
	SC_3 = 13.307 – 6.327 Log_{10}Fetch – 4.243 U2	0.56***	0.00	0.56
6S	TFD = 0.166 – 0.064 S4	0.64***	0.64	0.00
	RB = 5.147 – 1.948 S4 – 1.631 U2	0.57***	0.44	0.13
	SC_1 = 67.237 + 10.264 S4 + 10.456 U2 + 5.490 Log_{10}Fetch	0.86***	0.49	0.37
	SC_2= 7.955 – 6.745 S4 + 7.099 U3 + 3.394 S3	0.89***	0.19	0.06
	SC_3 = 15.055 – 9.114 U2	0.41***	0.00	0.41

Conclusion générale

« The only thing about Nature that is certain and absolute is patchiness in space and time» (Wu et Loucks 1995)

Cette thèse avait comme objectif principal de modéliser la structure des communautés de poissons lacustres en relation avec les facteurs environnementaux littoraux. La modélisation fut effectuée à l'aide d'une approche multiscalaire, c'est-à-dire en modifiant les attributs relatifs à l'échelle d'analyse spatiale. Dans un premier temps, l'utilisation d'une méthode d'analyse statistique tenant explicitement compte de la distance entre les unités d'échantillonnage a permis d'observer que les espèces littorales présentaient une variété de patrons de distribution s'échelonnant sur des distances géographiques variant de 100 m à plus de 2 km. L'interprétation de ces patrons de distribution géographique a montré que la distribution spatiale des espèces était associée à la relation fonctionnelle que ces espèces entretiennent avec leur environnement. Dans un deuxième temps, la modification du grain de l'échelle d'analyse a permis de vérifier l'impact de la taille des unités d'analyse sur la performance des modèles d'habitats et de mettre en évidence l'importance de la distribution et l'arrangement spatial des habitats sur la structure des communautés littorales. Les conclusions de ma thèse s'inscrivent dans une double perspective; d'une part, elles portent sur la description et la compréhension des patrons de distribution spatiale des espèces littorales et d'une autre part, elles portent sur la prédiction et s'inscrivent dans un contexte appliqué et prédictif de conservation.

RECENSEMENT VISUEL DES COMMUNAUTÉS DE POISSONS

L'étude de la structuration spatiale des communautés piscicoles littorales et de leur environnement nécessite une couverture spatiale complète et continue de la zone littorale des lacs. La technique de recensement visuel permet notamment ce type d'échantillonnage (Pratt and Fox 2001). Qualifiée de méthode non destructive, le recensement visuel permet un échantillonnage répété dans le temps (Hall and Werner 1977), à des endroits difficilement atteignables et en minimisant les perturbations de l'environnement dans lequel les recensements ont été effectués (Helfman 1983). L'observation visuelle ne peut toutefois pas être effectuée dans les lacs eutrophes, caractérisés par une visibilité réduite (< 2 m). La comparaison du recensement visuel avec la seine de rivage, une méthode d'échantillonnage couramment utilisée en lac, a permis d'établir les limites inhérentes au recensement visuel et d'encadrer le choix des descripteurs de la communauté de poissons utilisés dans les chapitres ultérieurs.

Parmi les descripteurs comparés, la majorité d'entre eux ne présentaient soit aucune différence significative entre les deux méthodes, soit un avantage pour le recensement visuel. Seules la densité totale et la biomasse totale, deux descripteurs fortement corrélés (Pearson $r = 0.91$; $N = 40$, $p \leq 0.001$), furent visuellement sous-estimées (de 50% et 40% respectivement). Cette divergence entre les deux méthodes fut principalement attribuable à la stratégie d'échantillonnage employée lors du comptage des individus. En effet, comme le recensement des individus à chaque site d'échantillonnage s'est effectué par classe d'individus, l'abondance maximale d'une espèce pouvant être observée à chaque site saturait à 10 individus alors qu'il n'y avait aucun plafond pour la seine. L'utilisation de ces deux descripteurs dans les chapitres ultérieurs de la thèse, malgré les divergences observées se justifie par deux raisons. D'abord, cette lacune en ce qui concerne l'échantillonnage n'a vraisemblablement affectée que *L. gibbosus* qui présentait de fortes abondances à chaque site. Ensuite, malgré la capture d'un plus grand nombre d'individus avec la seine, nous avons observé une corrélation significative (Pearson $r = 0.57$; $N = 40$, $p \leq 0.001$) entre les observations obtenues par la seine et celles obtenues par le recensement visuel pour l'ensemble des espèces dans l'ensemble des sites.

STRUCTURE SPATIALE HIÉRARCHISÉE DES COMMUNAUTÉS LITTORALES

L'utilisation d'une technique d'analyse statistique récente, les *Coordonnées Principales de Matrices Voisines* (CPMV; Borcard and Legendre 2002), a permis de détecter et de quantifier des patrons de distribution spatiale associés aux échelles intermédiaires, rarement explorées dans les études intra-lacs. La communauté piscicole littorale du Lac Drouin présentait une variabilité spatiale fluctuant sur plusieurs échelles spatiales. Cette variabilité fut classifiée en quatre sous-modèles, représentant des patrons de distribution géographique hiérarchisés variant de 2 km (échelle très large) à moins de 100 m (échelle fine). Les patrons de distribution associés à certaines échelles spatiales furent corrélés à des variables environnementales spécifiques, suggérant ainsi la présence de processus écologiques hiérarchisés dépendant de l'échelle spatiale. Ainsi, la communauté de poissons littoraux du Lac Drouin était influencée par le fetch, un processus physique défini comme une mesure d'exposition aux vents prédominants et agissant à une échelle spatiale très large (Randall et coll. 1996). Le fetch peut également influencer la répartition des structures physiques formant les habitats (p . ex. sédiments, substrats, macrophytes; Cyr 1998) sur des échelles spatiales plus fines. Ces structures physiques seraient à leur tour impliquées dans la distribution spatiale des espèces. Nous avons noté une diminution de l'importance des variables physiques dans la structure de la communauté de poissons en corrélation avec une diminution de l'échelle spatiale. Cette observation supporte les conclusions jusqu'à présent émises par différentes études (Ricklefs 1987, Pinel-Alloul et coll. 1999), énonçant que les facteurs abiotiques seraient davantage impliqués dans le contrôle des communautés littorales à échelles spatiales larges alors que les facteurs biotiques (p. ex. interactions biologiques) le seraient davantage aux échelles spatiales plus fines.

En se basant sur les prémisses statuant que les espèces partageant les mêmes habitats ont des patrons de distribution spatiale similaires (Morris 1987), nous avons tenté d'expliquer les patrons de distribution spatiale des espèces en suggérant une description spatiale hiérarchisée de la structure de la communauté de poissons du Lac Drouin. Cette proposition supposait une classification fonctionnelle des espèces en fonction de l'étendue des échelles spatiales auxquelles elles étaient distribuées (Kolasa 1989). Ainsi, les espèces dites généralistes montraient des patrons de distributions sur des échelles spatiales très larges ou plusieurs patrons de distribution spatiale sur différentes échelles spatiales. Par opposition, les espèces spécialistes présentaient des patrons de distribution spatiale aux échelles plus fines ou sur une seule échelle spatiale.

SÉGRÉGATION FONCTIONNELLE DES HABITATS

Les suppositions, portant sur la distribution spatiale hiérarchisée des espèces selon leur relation fonctionnelle avec l'environnement, furent l'objet d'une étude plus approfondie au Chapitre 3. Étant donné l'influence limitée des variations saisonnières suggérées au Chapitre 2, les analyses furent effectuées sur les données récoltées à la fin de l'été, moment où les variables environnmentales montraient une association légèrement plus élevée avec la communauté de poissons. Nous avons observé que les traits morphologiques et comportementaux des espèces déterminaient le type de patron de distribution spatiale de ces espèces. D'une part, l'association de certains traits des espèces permit de regrouper les espèces en trois groupes fonctionnels associés à la position de la bouche et au niveau où les espèces se nourrissent dans la colonne d'eau (c.-à-d.. ségrégation verticale). D'autre part, les groupes fonctionnels présentaient des différences en ce qui a trait à leur association avec différents types d'habitats, suggérant ainsi une ségrégation à la fois verticale (colonne d'eau) et horizontale (habitat; Eadie and Keast 1984). Toutefois, les corrélations observées entre les traits des espèces et les caractéristiques environnementales étant très faibles (0.057 à 0.197), l'interprétation des résultats reste en partie spéculative. Des études futures effectuant des mesures morphologiques et comportementales à partir d'observations directes permettraient de valider ou d'infirmer ces interprétations.

Alors que le degré de complexité structurelle des habitats différait entre les échelles spatiales, une certaine persistance en ce qui a trait aux associations entre les traits biologiques des espèces, formant les groupes fonctionnels, fut observée entre les échelles spatiales. Ainsi, 94% (Lac Drouin) et 90% (Lac Paré) des traits des espèces appartenaient aux mêmes groupes fonctionnels à très grande et à grande échelle spatiale. Ce résultat suggère que la classification des espèces de poissons littoraux en supra-unités trophiques fonctionnelles se situant au-dessus de la représentation taxonomique traditionnelle représenterait une unité d'observation appropriée pour l'étude des communautés littorales de poissons. D'une perspective de conservation, cette conclusion s'accorde avec le concept de description opérationnelle des écosystèmes, récemment préconisé par certaines études favorisant une gestion par l'entremise d'espèces indicatrices associées aux groupes fonctionnels (voir Davic 2003). Ces études supposent que les processus écologiques impliqués dans l'organisation des écosystèmes seraient davantage liés aux interactions intra et inter-groupes fonctionnels qu'aux interactions intra et inter-spécifiques.

LA TACHE : UNE UNITÉ D'ANALYSE APPROPRIÉE

L'utilisation d'une approche multiscalaire aux chapitres précédents a permis de mettre en évidence que les espèces de poissons répondaient fonctionnellement à la complexité structurale (à plusieurs échelle spatiale) de la zone littorale. La diversité des patrons de distribution des espèces sur plusieurs échelles géographiques suggérait notamment l'importance des interactions entre les caractéristiques environnementales et le contexte spatial dans lequel les espèces évoluent. Dans cette perspective, la comparaison des modèles prédictifs développés à partir de trois unités d'analyses (site, multiple et tache) représentant des étendues géographiques différentes, a permis de déceller les rôles structurels et fonctionnels que peut jouer l'arrangement spatial des taches d'habitat sur la structure des communautés de poissons (Weaver et coll. 1997, Kocik and Ferreri 1998). Les modèles d'habitats élaborés à l'aide de l'approche par taches d'habitats expliquaient de 14% à 28% plus de variabilité de la communauté de poissons que les modèles élaborés à l'aide de l'approche classique par site. Bien que la performance (R^2) des modèles développés à partir de l'approche par tache était comparable aux modèles élaborés avec l'approche multiple, les modèles par tache présentaient une plus grande stabilité (c.-à-d., plus petits écarts-types). Ces résultats suggèrent qu'en agglomérant en taches de différentes tailles les sites présentant les mêmes structures physiques, nous avons intégré des informations relatives aux exigences biologiques des espèces et peut-être avons réduit le biais de la perception anthropomorphique d'un habitat (Bult et coll. 1998). En effet, la tache représente le patron de distribution spatiale le plus couramment observé en lacs (Weaver et coll. 1997). Pour plusieurs espèces, les taches d'habitats constituent des aires nécessaire à l'accomplissement de leur cycle de vie (Mittelbach 1981, Tabor and Wurtsbaugh 1991, Diehl 1993).

Nos conclusions corroborent les résultats obtenus récemment par d'autres études qui ont souligné l'importance de la taille et de l'arrangement spatial des différents habitats sur les relations poissons-environnement (Lewis et coll. 1996, Kocik and Ferreri 1998, Essington and Kitchell 1999, Wiens 2002). Par exemple, la fragmentation de l'habitat en taches de petites tailles, en comparaison à des taches de tailles plus grandes favorisait l'abondance de poissons de petites tailles (Weaver et coll. 1997). Dans un contexte de fragmentation des habitats littoraux des poissons, la tache nous apparaît comme unité d'observation intéressante puisqu'elle permet d'intégrer différents éléments biologiques de la communauté de poissons (composition et structure en taille) et qu'elle permet une description quant à la structure (taille et arrangement spatial) et la qualité des habitats littoraux (Franklin 1995).

CONSERVATION DES HABITATS LITTORAUX LACUSTRES

Les résultats de cette thèse contribuent à l'élaboration une nouvelle perspective en regard à la problématique actuelle portant sur la conservation des habitats dans la zone littorale des lacs. L'association entre les groupes fonctionnels et les caractéristiques environnementales des habitats propose l'attribution d'une identité et d'une valeur écologique aux habitats définissant ainsi la zone littorale comme une « diversité fonctionnelle » d'habitats. Parallèlement, les résultats de la thèse soulignent que la taille d'un habitat ne saurait représenter le seul critère au maintien de cette diversité fonctionnelle des poissons dans un lac. L'interaction de la taille, de la distribution spatiale des taches et des caractéristiques environnementales (intrinsèques et extrinsèques) associées à ces taches sont autant de critères nécessaires au maintien de la diversité des populations littorales. D'un point de vue appliqué, ce genre d'information suggère l'idée d'une gestion par taches d'habitat, dont la conservation par section d'une certaine proportion de différents types d'habitat favoriserait le maintien de la diversité fonctionnelle de la zone littorale d'un lac.

STRATÉGIES D'ÉCHANTILLONNAGE

La mise en commun des résultats obtenus par l'analyse des CPMV (Chapitre 2) et par l'analyse des taches d'habitat (Chapitre 4) suggère des modifications aux stratégies d'échantillonnage couramment utilisées lors de l'étude de la structure des communautés de poissons littoraux dans les lacs. Alors que la majorité des stratégies d'échantillonnage préconise le choix de quelques sites définit par des caractéristiques environnementales spécifiques (p. ex. macrophytes, substrat, pente) distribuées au hasard sur le périmètre du lac, cette thèse recommande plutôt un devis expérimental basé sur l'échantillonnage de sections entières de la zone littorale constituées d'un ensemble de sites contigus possédant un éventail de caractéristiques environnementales. L'ensemble des sections devrait représenter au minimum 10 à 20 % du périmètre total d'un lac puisque c'est vraisemblablement à partir de ce seuil que l'échantillonnage de la zone littorale englobe une proportion représentative d'habitats associés aux populations de poissons. Ces sections devraient être distribuées sur tout le périmètre du lac, notamment pour tenir compte de l'influence de l'exposition aux vents dominants sur la structure des communautés.

ORIGINALITÉ

L'originalité de cette thèse s'inscrit principalement dans son caractère intégrateur à plusieurs niveaux. D'abord, l'utilisation d'une nouvelle méthode d'échantillonnage continue permet d'intégrer entièrement la zone littorale des lacs, ce qui lui confère l'avantage de couvrir une grande diversité de variables environnementales et de vérifier l'influence multiscalaire des interactions entre ces variables environnementales et les communautés de poissons. Elle intègre également des concepts provenant de différentes disciplines écologiques telles, l'écologie des poissons, l'écologie numérique et l'écologie du paysage. D'ailleurs, l'union de ces trois disciplines a permis l'adoption d'une vision beaucoup plus spatialisée des interactions entre les espèces peuplant la zone littorale des lacs et leur environnement.

PERSPECTIVES ET AMÉLIORATIONS

D'un point de vue appliqué, la démonstration de l'importance de l'intégration de l'arrangement spatial dans les modèles prédictifs d'habitats de poissons ouvre la voie vers une modélisation spatialisée des relations poisson-habitat. Ce type de modélisation pourrait notamment faire appel à l'utilisation de système d'information géographique (SIG) basé sur la taille des taches d'habitats afin de répondre à d'importantes questions en conservation des habitats de poissons concernant l'impact d'une variation du nombre, de la taille, de la nature et de l'arrangement spatial des habitats sur la composition des assemblages et l'abondance des espèces littorales.

Les conclusions de cette thèse sont basées sur un nombre limité de lacs (n = 2) situés dans un région géographique présentant une histoire géologique spécifique. Dans ce contexte, la généralisation de nos conclusions serait hasardeuse. Il serait intéressant de vérifier la généralisation des résultats en augmentant le nombre de lacs et d'échantillonner des lacs présentant des tailles et même des ratios littoral/pélagique différents.

L'emphase de cette thèse a été mise principalement sur les variations spatiales des patrons de distribution des espèces de poissons. Il est toutefois reconnu que l'échelle temporelle détermine aussi fortement la structure des communautés des poissons littoraux. L'intégration d'une plus grande étendue temporelle (p. ex. distribution de nuit, distribution saisonnière), couplée à une augmentation de la spatialité (p. ex. distribution dans la colonne d'eau, distribution infra-littorale) permettrait d'obtenir un portrait beaucoup plus complet de la structure des communautés piscicoles lacustres. De plus, cette intégration accroîtrait la représentativité de certaines phases de vie des poissons (p. ex. larvaire) favorisant ainsi une plus grande couverture de la structure en taille des espèces.

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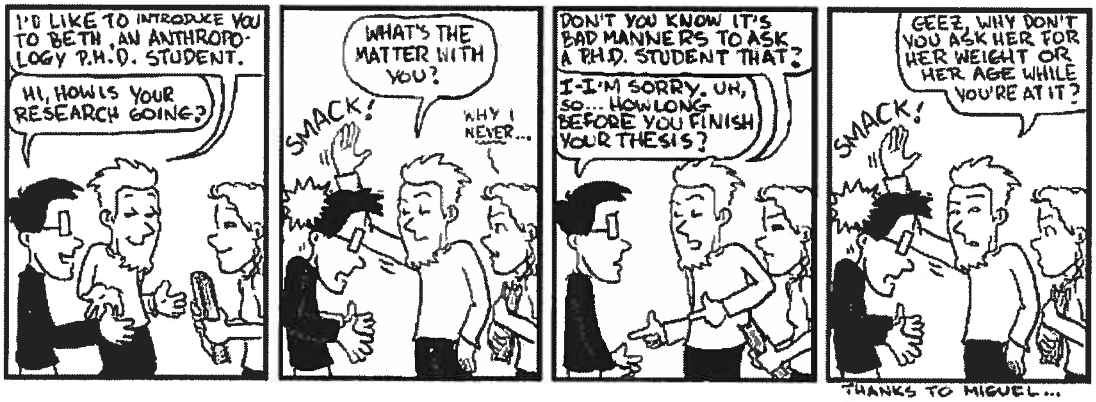

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