Littoral Fish Communities in Southern Quebec Lakes: Relationships with Limnological and Prey Resource Variables[1]

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We assessed species richness, biomass, and community type of littoral fish in 10 southern Quebec lakes in relation to several limnological and prey resource variables. Lake, yearly, and seasonal variation in biomass was evaluated by quantitative, replicated seining. Species richness averaged 12.8 in our lakes, and 24 species were collected overall. Total littoral fish biomass averaged 13.5 $g{\cdot}m^{-2}$ overall and varied significantly among lakes (range 6.1–26.9 $g{\cdot}m^{-2}$) and between early and late summer. Yellow perch (*Perca flavescens*), golden shiner (*Notemigonus crysoleucas*), and pumpkinseed (*Lepomis gibbosus*) occurred in all lakes and were the most abundant species overall, averaging 57% of the total fish biomass. Principal component ordination of littoral fish communities showed little evidence for aggregation of community types. Species richness was positively correlated with lake surface area ($r^2 = 0.62$), as has been shown in other studies. Total fish biomass was positively correlated with biomass of chironomids ($r^2 = 0.57$), which constituted 24% of the littoral invertebrate biomass in our lakes and are important prey of many fish species. We found no significant correlation between total fish biomass and total invertebrate biomass or between biomass of any of the dominant fish species and limnological or prey variables.

Nous avons évalué l'abondance des espèces, la biomasse et les types de communauté de poissons littoraux trouvés dans 10 lacs situés dans le sud du Québec en fonction de plusieurs variables limnologiques et ressources en proies. En procédant par sennage quantitatif et répété, nous avons évalué les variations saisonnières, annuelles et par lac de la biomasse. Nos lacs comptaient en moyenne 12,8 espèces et au total, 24 espèces ont été prélevées. La moyenne de la biomasse totale en poissons littoraux était globalement de 13,5 $g{\cdot}m^{-2}$; la biomasse variait significativement d'un lac à l'autre (entre 6,1 et 26,9 $g{\cdot}m^{-2}$) et entre deux périodes, soit le début et la fin de l'été. La perchaude (*Perca flavescens*), la chatte de l'est (*Notemigonus crysoleucas*) et le crapet soleil (*Lepomis gibbosus*) ont été trouvés dans tous les lacs; dans l'ensemble, c'étaient les espèces les plus abondantes, avec 57 % de la biomasse totale de poissons. Le classement par principales espèces des communautés de poissons littoraux n'a pas permis de mettre vraiment en évidence une aggrégation des types de communauté. Il existe une corrélation positive entre l'abondance des espèces et la superficie des lacs ($r^2 = 0{,}62$), comme on l'a établi ailleurs. Il existe aussi une corrélation positive entre la biomasse totale des poissons et la biomasse des chironomidés ($r^2 = 0{,}57$), qui correspondaient à 24 % de la biomasse des invertébrés littoraux dans nos lacs et qui sont aussi une proie importante pour de nombreuses espèces de poissons littoraux. Nous n'avons pas trouvé de corrélation significative entre la biomasse totale de poissons et la biomasse totale d'invertébrés non plus qu'entre la biomasse de toute espèce dominante donnée de poissons et les proies ou des variables limnologiques.

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Abundance and community composition of freshwater fishes have been topics of continued interest in fisheries ecology (Evans et al. 1987; Marshall and Ryan 1987; Wootton 1990). These communities have been examined using a number of different approaches, including intensive studies of a single or small number of systems (Wells 1977; Waters 1982; Lyons 1987, 1989; Elliott 1988; Johannes et al. 1989; Mills and Hurley 1990), comparative analyses of primarily literature data on biomass and fishery yields from many systems (Hanson and Leggett 1982; Kerr and Ryder 1988; Downing et al. 1990; Quiros 1990), and comparative analyses of fish species distributions from many systems (Rahel 1986; Jackson and Harvey 1989; Tonn et al. 1990; Hinch et al. 1991). Intensive studies frequently sample over an extended period of time, providing good estimates of temporal variability within the system. However, the range of variability encountered and the patterns of correlated responses among variables are difficult to extrapolate to other systems (Frost et al. 1988). Comparative analyses address spatial variation and patterns across many systems,

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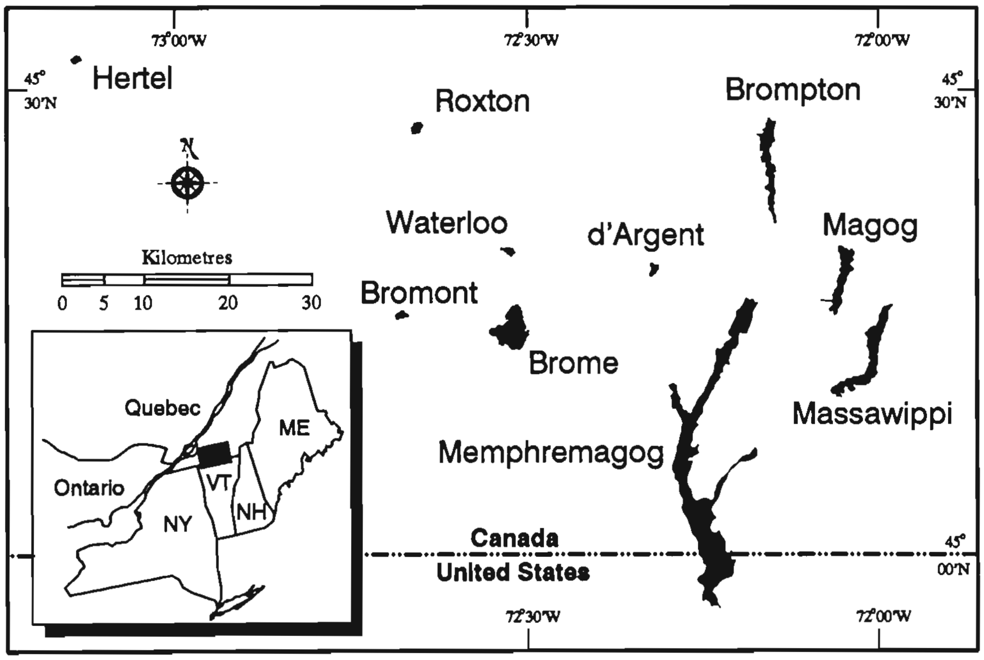

FIG. 1. Location of southern Quebec lakes sampled in this study. Lakes Bromont and Hertel are shown at twice actual size for clarity.

but often either ignore temporal variation by relying on single samples or assume temporal variation to be negligible by comparing samples or sample averages from different time periods. Few studies have examined spatial patterns of biomass and community composition across systems simultaneously with temporal variation (Hinch 1991), and we are aware of no such studies of littoral fish communities in lakes. Comparisons have been further hampered by the fact that many studies report only qualitative or relative abundances. Fewer still are studies that incorporate considerations for differences in gear efficiency and other sampling problems (Bayley 1985; Lyons 1987; Pierce et al. 1990).

The littoral zone fish fauna plays an important role in freshwater lake ecosystems (Northcote 1988). Abundance is typically greater than in other zones, and in many lakes, littoral species make up the bulk of the total fish community (Keast and Harker 1977; Werner et al. 1977). Littoral zone habitat and food resources are much more diverse than in other zones, potentially leading to complex relationships with the fish community. Intra- and interspecific interactions among littoral fishes are common, and the roles of predator, prey, and competitor undergo complex shifts in response to ontogeny, habitat, and resources (Mittelbach 1986). Littoral zone species are also frequently important as prey to larger, predominantly pelagic species (Lyons and Magnuson 1987). Characterization of patterns of biomass and community composition and development of empirical relations with limnological and prey resource variables should enhance our understanding of littoral fishes, just as similar efforts have yielded new insights with other components of aquatic systems (Peters 1986).

The purpose of this study was to assess the species richness, biomass, and community type of littoral zone fishes in 10 southern Quebec lakes in relation to several limnological and prey resource variables. Biomass was quantified using replicated littoral seining designed to evaluate both spatial (among-lake) as well as seasonal and yearly variation. Several limnological and prey resource variables were assessed concurrently with the fish sampling, and lake morphometric variables were obtained from the literature. We used principal components analysis to generate fish community, limnological, and prey community ordinations and explored relationships among these multivariate ordinations as well as bivariate relationships among individual variables.

Materials and Methods

Study Lakes

Our study was conducted in 10 lakes located in the Eastern Townships region of southern Quebec, Canada (Fig. 1). Several previous studies describe a variety of characteristics of these lakes, including pelagic zooplankton and phytoplankton (Pace 1984, 1986), littoral periphyton (Cattaneo 1987), sediments (Rowan et al. 1992), macrophytes (Chambers and Kalff 1985; Duarte and Kalff 1986; Anderson and Kalff 1988), benthos (Rasmussen 1988a, 1988b, 1993), growth of yellow perch (Boisclair and Leggett 1989a, 1989b, 1989c), and littoral fish sampling conditions (Pierce et al. 1990).

Estimating Fish Species Richness and Biomass

We sampled the littoral fish communities of each of the 10 lakes once in early summer and once in late summer during 1987 and 1988. The early summer period was from 18 June to 26 June in 1987 and from 4 July to 15 July in 1988. The late summer period was from 24 August to 17 September in 1987 and from 8 September to 22 September in 1988. Two replicate samples were taken in different locations at each lake during each sampling period. This sampling design allowed us to characterize the littoral fish communities and assess among-lake, yearly, and seasonal variation in biomass across the 10 lakes.

We used beach seines as described by Pierce et al. (1990) for all samples. In 1987, we used a 52 × 2.6 m knotless nylon (6-mm mesh) seine, with a continuous lead-core bot-

TABLE 1. Occurrence and mean biomass (untransformed) of fish species in the littoral zone of southern Quebec lakes. Species are listed in descending order of overall biomass. Numbers identifying lakes are given in Table 2.

Species	Common name	Lakes containing species	Mean biomass in lakes containing species (g·ha^{-1})
Perca flavescens	Yellow perch	All lakes	35 759
Notemigonus crysoleucas	Golden shiner	All lakes	22 293
Lepomis gibbosus	Pumpkinseed	All lakes	18 563
Moxostoma anisurum	Silver redhorse	7	86 296
Ameiurus nebulosus	Brown bullhead	All lakes	8 045
Catostomus commersoni	White sucker	All lakes	6 879
Esox lucius	Northern pike	1–7, 9, 10	7 590
Moxostoma valenciennesi	Greater redhorse	7	35 026
Esox niger	Chain pickerel	1–6, 8–10	2 693
Ambloplites rupestris	Rock bass	1, 3, 5–9	2 126
Fundulus diaphanus	Banded killifish	1–4, 8	1 852
Micropterus dolomieu	Smallmouth bass	1, 2, 4, 6–10	1 110
Hybognathus regius	Eastern silvery minnow	7	6 656
Semotilus corporalis	Fallfish	1, 3, 4, 7, 10	1 176
Pimephales notatus	Bluntnose minnow	1–4, 7–9	812
Notropis atherinoides	Emerald shiner	7, 8	2 583
Etheostoma nigrum	Johnny darter	1–3, 6–9	364
Luxilus cornutus	Common shiner	1, 2, 4, 8, 10	471
Micropterus salmoides	Largemouth bass	6, 8, 9	525
Semotilus atromaculatus	Creek chub	7, 10	541
Pomoxis nigromaculatus	Black crappie	9	675
Notropis hudsonius	Spottail shiner	2	270
Percina caprodes	Logperch	2, 7	81
Osmerus mordax	Rainbow smelt	6, 8	45

tom line, plastic floats along the top line, and a 2.6-m^3 bag in the center. In 1988, we used a seine of identical design but larger dimensions (100 × 3 m). The seine was deployed from a small boat in a semicircle extending out from the shoreline, enclosing an area of 430 m^2 in 1987 and 1600 m^2 in 1988. Depth at the deepest point of the enclosed area averaged 1.7 m. We pulled the seine to shore from both ends, with a diver and an assistant in the boat monitoring the progress of the seine. Captured fish were anesthetized immediately in 2-phenoxyethanol, put on ice, and frozen within a few hours. In the laboratory, fish were identified to species, measured (total length, TL) to the nearest millimetre, and weighed (wet) to the nearest 0.01 g. *Micropterus* and *Esox* species were measured (TL) immediately upon capture and released alive; wet weights for these species were estimated using equations in Carlander (1969) and Murphy et al. (1991). During the late summer sampling period in 1987 and both sampling periods in 1988, habitat and habitat-related variables such as macrophyte biomass, snags and seine rolling were quantified as described in Pierce et al. (1990).

We calculated biomass (wet grams per square metre) of individual species and the total fish community in each sample. Biomass estimates from the 1988 samples were corrected for variable capture efficiency using equations described in Pierce et al. (1990). The late summer samples from 1987 were corrected for capture efficiency using efficiency estimates obtained directly at the time of sampling. Efficiency estimates obtained from a given location tended to be similar, so we used the mean of all efficiency estimates from a given location as the correction for capture efficiency at that location in the 1987 early summer sampling period.

Estimating Limnological Conditions and Prey Resources

Water temperature, Secchi depth, chlorophyll *a* concentration, submerged littoral macrophyte biomass, and invertebrate prey biomass in each lake were sampled several times during the months of May–September in 1987 and 1988. Water temperatures were estimated using a combination of littoral and pelagic temperature profiles at 1-m depth intervals. Littoral temperature profiles were recorded near fish sampling areas from the surface to the bottom (approximately 3 m). Pelagic profiles were recorded at offshore locations from the surface to a depth of 3 m. Temperatures from individual profiles were averaged across depths, and these values were then averaged over the two years of sampling for each lake. Chlorophyll *a* concentrations were determined from integrated epilimnetic water samples obtained from offshore locations using a tube sampler; triplicate 500-mL subsamples were vacuum-filtered (65 μm) and frozen in the field and extracted in the laboratory (Strickland and Parsons 1972). Secchi depths were measured concurrently with water sampling. We sampled submerged littoral macrophyte biomass concurrently with fish samples as described in Pierce et al. (1990). Littoral sediment-dwelling and epiphytic macroinvertebrate prey were sampled as described in Rasmussen 1988a). Organisms were identified, counted, and measured for conversion to biomass using length–mass regressions (Smock 1980; C.W. Osenburg, Department of Integrative Biology, University of California, Berkeley, CA 94720, USA, unpublished data; J.B. Rasmussen, unpublished data). Littoral zooplankton prey were sampled at 07:00 by triplicate bottom-to-surface vertical hauls with a 30.5-cm-diameter, 75-μm-mesh net. Depths were recorded to the nearest 0.1 m and were generally near 3 m. A filtering efficiency of 46%, estimated by several calibrations with pooled Schindler–Patalas trap samples taken at 1-m intervals, was applied as a correction factor in biomass calculations. Samples were preserved in a sucrose–Formalin solution (Haney and Hall 1973). Organisms in subsamples (usually 10%) were identified and counted, and at least 30 individuals of each taxon were measured for conversion to biomass using length–mass regressions (Dumont et al. 1975; Culver et al. 1985).

Conductivity, surface area, mean depth, maximum depth, and water residence time data from each lake were obtained from published studies (Rasmussen 1988a; Rowan et al. 1992).

Statistical Analyses

Data were analyzed using analysis of variance (ANOVA), principal components analysis (PCA) ordination, correlation, and regression analysis. Lake, yearly, and seasonal variation in biomass of the total littoral fish community and dominant species was evaluated with three-way ANOVA, using $\log_{10}(x + 1)$ transformed data. We used three separate PCA ordinations to compare the 10 lakes on the basis of littoral fish communities, limnological conditions, and invertebrate prey communities. Lake averages of $\log_{10}(x + 1)$ transformed data were used as input variables for ordinations, and principal components were extracted from covariance matrices. For the fish community ordination, we used the eight species found in eight or more of the lakes, including yellow perch (*Perca flavescens*), golder shiner (*Notemigonus crysoleucas*), pumpkinseed (*Lepomis gibbosis*), brown bullhead (*Ameiurus nebulosus*), white sucker (*Catostomus commersoni*), northern pike (*Esox lucius*), chain pickerel (*Esox niger*), and smallmouth bass (*Micropterus dolomieu*). These eight species accounted for 75% of the littoral fish biomass estimated across all lakes. For the limnological ordination, we used chlorophyll *a*, Secchi depth, littoral macrophyte biomass, temperature, conductivity, surface area, mean depth, maximum depth, and water residence time. For the prey community ordination, we used biomass (wet grams per square metre) of chironomids, trichopterans, ephemeropterans, oligochaetes, gastropods, pelecypods, amphipods, and zooplankton. These groups accounted for over 95% of the littoral invertebrate biomass estimated across all lakes. Relationships of principal components between ordinations and of principal components with individual variables were explored using correlation analysis. Linear regressions were generated to describe relationships of littoral fish species richness and biomass with limnological and prey resource variables. All analyses were performed using the ANOVA, CORR, PRINCOMP, and REG procedures of SAS (SAS Institute Inc. 1988).

Results

Fish Species Richness

Twenty-four species were present in our samples (Table 1). All are considered native to this zoogeographic region, accounting for roughly 25% of the known species inhabiting the St. Lawrence River drainage (Underhill 1986). Overall species richness of individual lakes ranged from 8 to 17, averaging 12.8 (Table 2). Species richness of individual samples ranged from 2 to 12, averaging 7.6 across all sam-

TABLE 2. Littoral fish biomass and species richness, invertebrate prey biomass, and limnological characteristics in southern Quebec lakes. All data are untransformed; biomass data are wet mass.

Lake	Lake No.	Number of littoral fish species	Mean littoral fish biomass ($g \cdot m^{-2}$)	Mean littoral benthos biomass ($g \cdot m^{-2}$)	Mean littoral zooplankton biomass ($g \cdot m^{-2}$)	Mean littoral macrophyte biomass ($g \cdot m^{-2}$)	Mean chlorophyll *a* concentration ($\mu g \cdot L^{-1}$)	Mean Secchi depth (m)	Mean summer water temperature (°C)	Surface area (ha)	Mean depth (m)
Brompton	1	14	10.0	15.2	0.14	1896	2.39	4.0	21.0	1191	11.5
Brome	2	14	7.0	53.8	0.13	1101	6.74	3.2	20.1	1452	5.7
Bromont	3	12	11.4	63.4	0.91	3018	8.65	2.2	21.0	50	5.2
d'Argent	4	12	6.6	15.0	0.17	818	3.64	3.1	21.1	96	4.6
Hertel	5	8	10.7	43.3	0.14	1781	2.53	3.7	18.1	29	4.7
Magog	6	12	26.9	60.1	0.07	3302	5.46	2.8	18.5	1080	9.7
Massawippi	7	17	22.5	9.3	0.71	1773	2.70	3.6	17.5	1790	40.2
Memphremagog	8	15	6.1	38.6	0.20	2281	2.45	3.0	18.9	9010	19.8
Roxton Pond	9	13	16.0	29.5	0.46	1435	7.73	2.2	19.7	179	3.2
Waterloo	10	11	17.6	62.7	0.50	2408	21.54	0.9	21.0	150	2.9

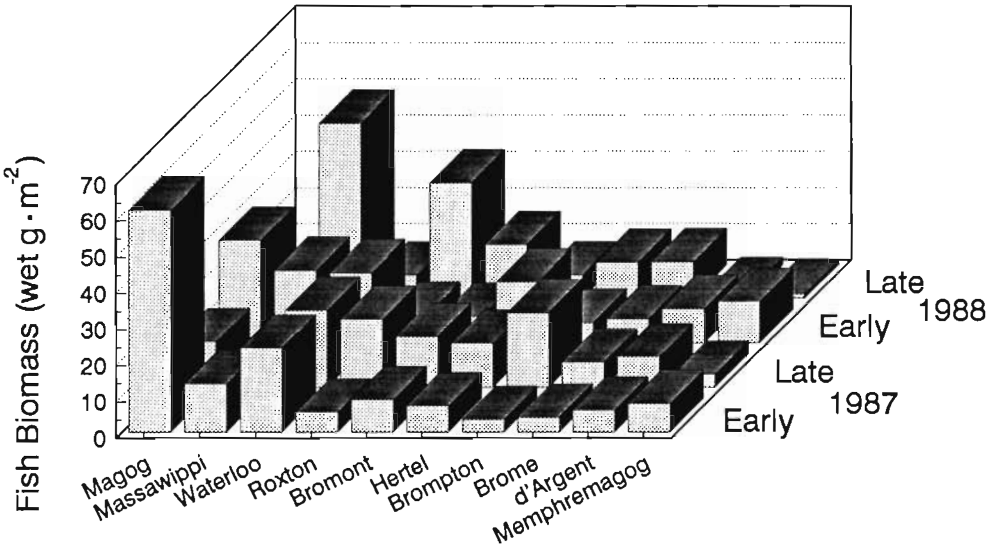

FIG. 2. Total fish biomass (untransformed) in the littoral zone of southern Quebec lakes during early and late summer of 1987 and 1988. Lakes are arranged in descending order of overall total biomass from left to right. Bars are means from two replicate samples.

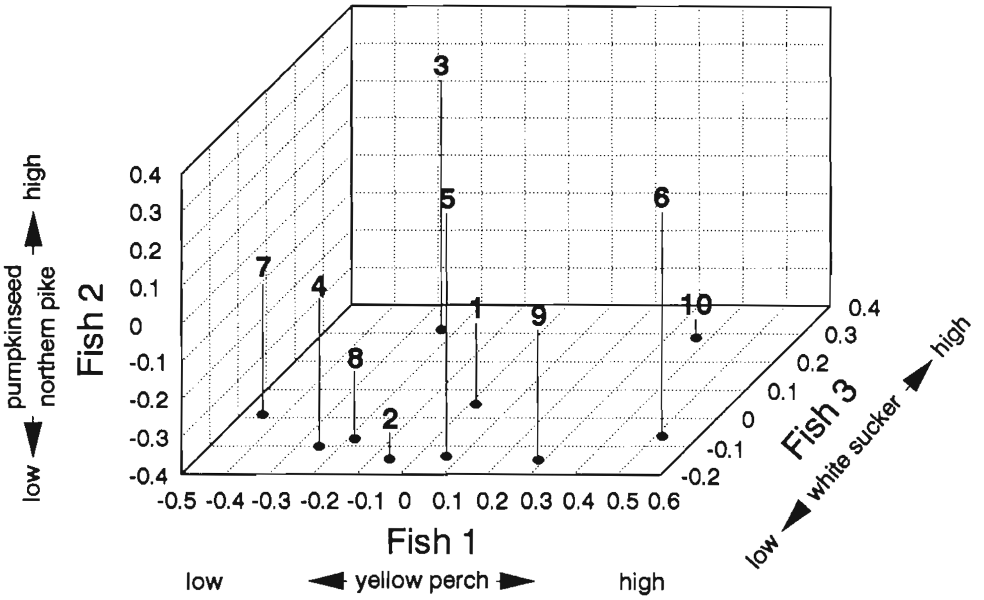

FIG. 3. Principal component ordination of littoral fish communities in southern Quebec lakes. Lakes are identified by numbers in Table 2.

ples. Individual samples contained an average of 61% of all species collected in their respective lakes over the course of the study. Five species (yellow perch, golder shiner, pumpkinseed, brown bullhead, and white sucker) were present in all 10 lakes. Three additional species were collected in at least eight of the 10 lakes. Five species were collected in only one lake.

Fish Biomass

Biomass of the total littoral fish community averaged 13.5 $g \cdot m^{-2}$ across all lakes. Mean total biomass varied more than fourfold among individual lakes, ranging from 6.1 to 26.9 $g \cdot m^{-2}$ (Table 2). Yellow perch, golden shiner, and pumpkinseed were the overall dominant species (Table 1), together accounting for 57% of the total fish biomass.

Total fish biomass varied significantly among lakes and between seasons, with the season of greatest biomass differing among lakes (Fig. 2; Table 3). Lakes Magog and Memphremagog had considerably greater littoral fish biomass in early summer than late summer whereas the pattern was reversed in Lakes Brompton, Bromont, and Roxton. Year effects were less pronounced than seasonal effects, with the exception of Lakes Magog and Massawippi. The three dominant littoral species showed the same general pattern of biomass across the 10 lakes: either strong lake × season interaction (yellow perch and golden shiner) or strong lake and season main effects (pumpkinseed) (Table 3).

Fish Community Ordination

PCA ordination of the littoral fish communities resulted in a general pattern of lakes scattered widely in principal component space, with little evidence of aggregation of com-

TABLE 3. Summary of ANOVAs testing the effects of lake (L), year (Y), and season (S) on biomass of total fish, yellow perch, golden shiner, and pumpkinseed in the littoral zone of southern Quebec lakes. Degrees of freedom for sources of variation are as follows: L, 9; Y, 1; S, 1; L × Y, 9; L × S, 9; Y × S, 1; L × Y × S, 9. Error mean squares for individual ANOVAs are as follows: total fish, 0.0382; yellow perch, 0.0288; golden shiner, 0.0646; pumpkinseed, 0.0321. Asterisks indicate significant effects: *$0.05 > P \geq 0.01$, **$0.01 > P \geq 0.001$, ***$0.001 > P \geq 0.0001$, ****$P < 0.0001$.

Group or species	Source of variation	F	P
Total fish	L	6.73	<0.0001****
	Y	0.11	0.746
	S	0.82	0.370
	L × Y	2.29	0.035*
	L × S	7.33	<0.0001****
	Y × S	4.95	0.032*
	L × Y × S	1.50	0.181
Yellow perch	L	20.42	<0.0001****
	Y	<0.01	0.990
	S	12.24	0.001**
	L × Y	3.07	0.007**
	L × S	6.18	<0.0001****
	Y × S	0.87	0.357
	L × Y × S	1.25	0.295
Golden shiner	L	4.54	0.0004***
	Y	4.44	0.041*
	S	2.47	0.124
	L × Y	2.09	0.054
	L × S	5.84	<0.0001****
	Y × S	0.08	0.773
	L × Y × S	1.14	0.356
Pumpkinseed	L	8.13	<0.0001****
	Y	<0.01	0.978
	S	13.53	0.0007***
	L × Y	1.23	0.305
	L × S	2.18	0.045*
	Y × S	0.06	0.808
	L × Y × S	1.78	0.102

TABLE 4. Correlations of fish species biomass with principal components from the PCA of littoral fish communities in southern Quebec lakes. P values are given in parentheses; % of variance explained is given at the bottom of the table.

	Principal component		
Species	Fish 1	Fish 2	Fish 3
Yellow perch	0.91 (0.0002)	−0.36 (0.308)	−0.05 (0.894)
Golden shiner	0.75 (0.013)	0.48 (0.158)	−0.15 (0.676)
Pumpkinseed	0.50 (0.143)	0.80 (0.006)	−0.05 (0.898)
Brown bullhead	0.56 (0.091)	−0.03 (0.932)	0.67 (0.033)
White sucker	0.05 (0.901)	0.04 (0.911)	0.98 (0.0001)
Northern pike	0.15 (0.687)	0.77 (0.009)	−0.04 (0.920)
Chain pickerel	0.42 (0.225)	0.26 (0.464)	0.14 (0.700)
Smallmouth bass	−0.56 (0.095)	−0.15 (0.671)	−0.04 (0.921)
% variance explained	46	25	14

munity types (Fig. 3). Communities in Lakes Bromont, Magog, and Waterloo appeared to be the most atypical among the 10 lakes. Principal component 1 (Fish 1) explained 46% of the variance and largely reflected biomass of yellow perch (Table 4), the most abundant species overall. Fish 1 was also positively correlated with biomass of golden shiner, the second most abundant species overall. Principal component 2 (Fish 2) explained 25% of the variance and reflected biomass of pumpkinseed, the third most abundant species overall, and northern pike. Principal component 3 (Fish 3) explained 14% of the variance and largely reflected biomass of white sucker. Fish 3 was also positively correlated with biomass of brown bullhead.

Limnological Conditions and Prey Resources

Mean limnological conditions and invertebrate prey biomass varied considerably among lakes, ranging from roughly fourfold variation in macrophyte biomass and Secchi depth to well over two orders of magnitude in surface area (Table 2). In contrast, mean summer water temperatures were fairly consistent among lakes, varying by only a few degrees.

Limnological and Prey Community Ordinations

PCA ordinations of the lakes based on limnological variables (Fig. 4a) and prey communities (Fig. 4b) revealed patterns broadly similar to the fish community ordination; lakes were widely scattered in principal component space and there was little evidence of aggregation. Principal component 1 (Limn 1) from the limnological ordination explained 76% of the variance and reflected lake size, correlating positively with surface area, mean depth, maximum depth, and water residence time (Table 5). Principal component 2 (Limn 2) explained 14% of the variation and appeared to reflect trophic conditions, correlating positively with chlorophyll *a*, macrophyte biomass, and conductivity and negatively with Secchi depth. The largest lakes in our data set tended toward intermediate trophic conditions (Fig. 4a).

Principal component 1 (Prey 1) from the prey community ordination (Fig. 4b) explained 40% of the variance and largely reflected biomass of molluscs, correlating positively with biomass of gastropods and pelecypods (Table 6). Molluscs accounted for over 50% of the littoral invertebrate prey biomass overall. Principal component 2 (Prey 2) explained 27% of the variance and reflected biomass of chironomids (Table 6), which accounted for 24% of the littoral invertebrate prey biomass overall.

Fish Community Relationships with Limnological Conditions and Prey Resources

The strongest relationships of fish communities with other lake characteristics were between fish species richness and measures of lake size (Fig. 5 and 6). Species richness was positively correlated with the principal component (Limn 1) expressing lake size (Fig. 5). Likewise, species richness was positively correlated with lake surface area and is shown

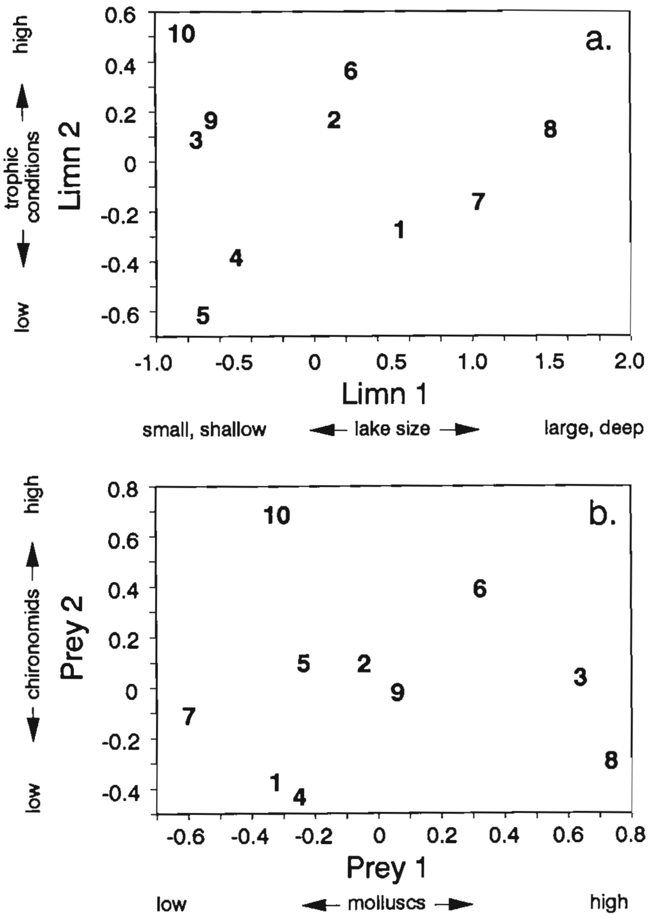

FIG. 4. Principal component ordinations of southern Quebec lakes based on (a) limnological variables and (b) invertebrate prey communities. Lakes are identified by numbers in Table 2.

in Fig. 6 plotted logarithmically to facilitate comparisons with two previous studies in Canadian lakes. Our species richness values compared well at the upper end of the lake size range, but were higher in smaller lakes than in previous studies. Species richness was also positively correlated with the other variables related to lake size: mean depth (r = 0.75, P = 0.013), maximum depth (r = 0.74, P = 0.015), and water residence time (r = 0.64, P = 0.044). No other significant correlations with species richness were seen.

We also found significant relationships of fish biomass with prey biomass. The principal component (Fish 1) expressing yellow perch and golden shiner biomass was positively correlated with the principal component (Prey 2) expressing chironomid biomass (Fig. 7), suggesting a relationship between the dominant community type and a major prey type. Total fish biomass was also positively correlated with Prey 2 (r = 0.69, P = 0.029) and, as expected from the very strong influence of chironomids on Prey 2 (Table 6), total fish biomass was positively correlated with chironomid biomass (Fig. 8). We found no significant correlation between total fish biomass and total invertebrate prey biomass (r = 0.01, P = 0.972). We then compared our data with Hanson and Leggett's (1982) empirical model of fish biomass based on the ratio of benthos biomass to mean depth (Fig. 9). As shown in Fig. 9, the correlation of total fish biomass with benthos·mean depth^{-1} as well as fit of our data to the model was poor.

TABLE 5. Correlations of limnological variables with principal components from the PCA of limnological data in southern Quebec lakes. P values are given in parentheses; % of variance explained is given at the bottom of the table.

	Principal component	
Variable	Limn 1	Limn 2
Chlorophyll *a*	−0.61	0.73
	(0.059)	(0.016)
Secchi depth	0.52	−0.74
	(0.125)	(0.015)
Macrophyte biomass	0.25	0.77
	(0.479)	(0.009)
Summer water temperature	−0.48	0.20
	(0.157)	(0.571)
Conductivity	0.24	0.67
	(0.504)	(0.034)
Surface area	0.95	0.23
	(0.0001)	(0.523)
Mean depth	0.91	−0.15
	(0.0003)	(0.687)
Maximum depth	0.97	−0.18
	(0.0001)	(0.624)
Water residence time	0.81	−0.24
	(0.004)	(0.500)
% variance explained	76	14

TABLE 6. Correlations of invertebrate prey biomass with principal components from the PCA of prey community data in southern Quebec lakes. P values are given in parentheses; % of variance explained is given at the bottom of the table.

	Principal component	
Taxon	Prey 1	Prey 2
Chironomids	−0.02	0.95
	(0.958)	(0.0001)
Trichopterans	0.39	0.09
	(0.259)	(0.806)
Ephemeropterans	−0.18	−0.42
	(0.628)	(0.231)
Oligochaetes	0.18	0.43
	(0.610)	(0.217)
Gastropods	0.76	0.32
	(0.011)	(0.375)
Pelecypods	0.93	−0.20
	(0.0001)	(0.581)
Amphipods	0.64	0.17
	(0.046)	(0.641)
Zooplankton	0.01	0.40
	(0.981)	(0.247)
% variance explained	40	27

Discussion

Species richness in the 10 lakes we studied was roughly comparable with values from other studies in North American lakes at similar latitude (Schneider 1981; Tonn and Magnuson 1982; Eadie and Keast 1984; Rahel 1986; Matuszek and Beggs 1988; Jackson and Harvey 1989). Previous work in our 10 study lakes produced similar species lists, but fewer

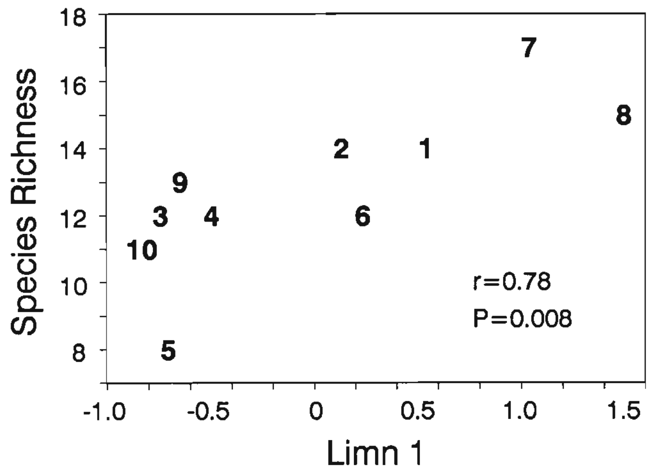

FIG. 5. Relationship of fish species richness in the littoral zone of southern Quebec lakes with scores from the first principal component (Limn 1) of the limnological ordination. Limn 1 represents variables related to lake size. Lakes are identified by numbers in Table 2.

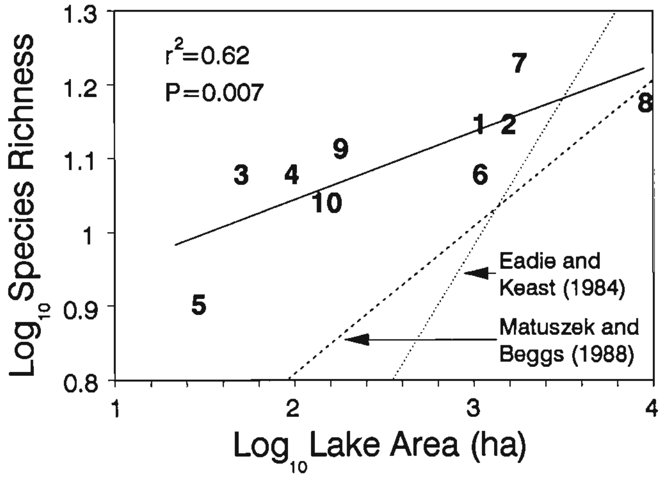

FIG. 6. Relationship of fish species richness in the littoral zone of southern Quebec lakes with lake surface area. The regression equation is $Y = 0.873 + 0.087X$; Y and X are $\log_{10}$ transformed values. Dotted and dashed lines represent relationships from previous studies for comparison. Lakes are identified by numbers in Table 2.

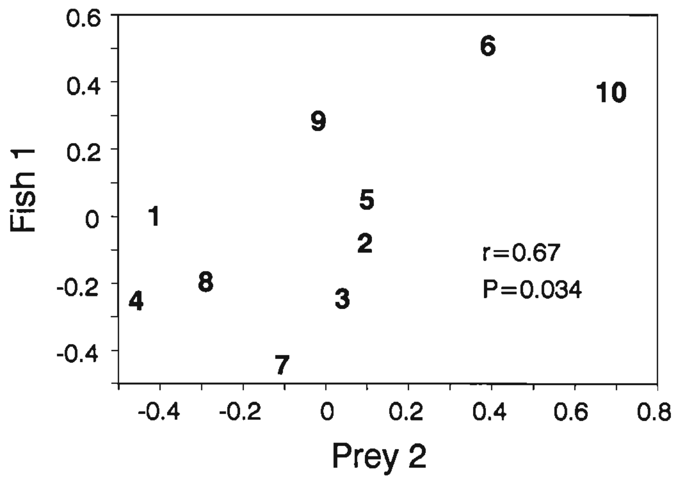

FIG. 7. Relationship of scores from the first principal component (Fish 1) of the fish community ordination with scores from the second principal component (Prey 2) of the prey community ordination in southern Quebec lakes. Fish 1 primarily represents abundance of yellow perch. Prey 2 primarily represents abundance of chironomids. Lakes are identified by numbers in Table 2.

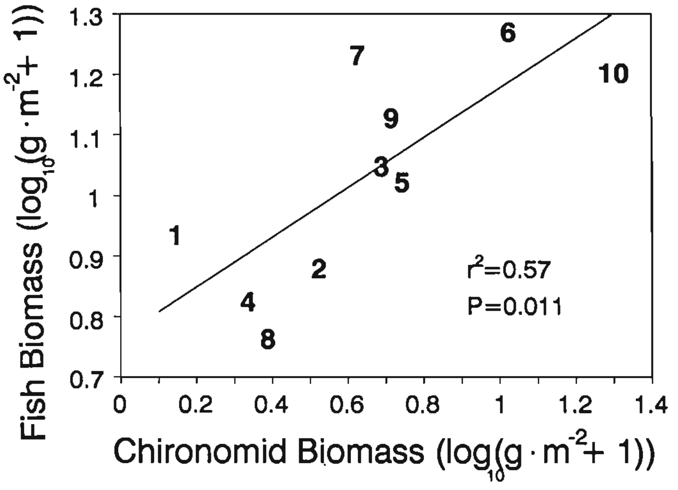

FIG. 8. Relationship of mean total fish biomass with mean chironomid biomass in the littoral zone of southern Quebec lakes. The regression equation is $Y = 0.770 + 0.404X$; Y and X are transformed as indicated. Lakes are identified by numbers in Table 2.

species were collected in all cases. Using similar sampling methods but half the number of samples (four), Boisclair and Leggett (1989c) reported species richness averaging 78% of our values. This percentage is roughly intermediate between our single-sample percentage (61%) and our total species richness (100%) values based on eight samples. This suggests that, despite coverage of large areas of the littoral zone in a single haul, numerous seine samples are necessary to detect the presence of rarer species. Provincial gillnet surveys (Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de l'Estrie, 85 rue Holmes, Sherbrooke, QC J1E 1S1, Canada) also reported species richness averaging 78% of our values. Focusing on sport fish, their species lists included pelagic and offshore species (e.g., lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), walleye (*Stizostedion vitreum*)) absent in our samples, but missed many of the smaller littoral species listed in Table 1. When compared with the combined species lists from all studies in the 10 lakes, our lists contained an average of 84% of the total species known to inhabit the respective lakes. Clearly, our intensive littoral sampling produced reasonably good estimates of species richness in these lakes. Large, deep lakes containing many offshore pelagic species require supplemental techniques.

Although the exact form of the relationship differed somewhat from previous studies (Fig. 6), our data confirmed the positive correlation of species richness with lake size described in previous work. Increased habitat diversity in larger lakes appears to be a likely causal factor producing this relationship (Eadie and Keast 1984; Matuszek and Beggs 1988). Our species richness values in larger lakes were very similar to those in lakes of comparable size from previous studies, but tended to be higher in smaller lakes (Fig. 6; see also fig. 5 in Jackson and Harvey 1989). These differ-

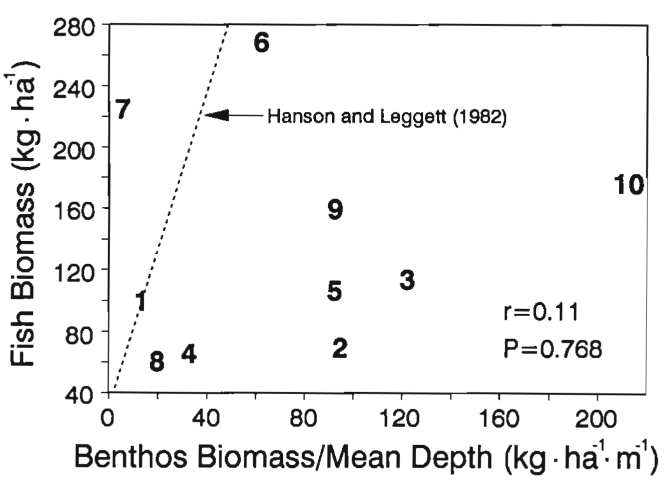

FIG. 9. Relationship of mean total fish biomass in the littoral zone of southern Quebec lakes with the ratio of mean benthos biomass to mean depth. The dashed line represents the relationship of Hanson and Leggett (1982) for comparison. Lakes are identified by numbers in Table 2.

ences may reflect differences in sampling methods; with the exception of the study by Eadie and Keast (1984), species richness data in other studies were obtained from a variety of sampling gears. Alternatively, differences in the form of the species richness – lake size relationship could be due to zoogeographical differences among study areas, as demonstrated by Jackson and Harvey (1989).

Our estimates of mean fish biomass in the 10 study lakes were well within the range of published values from several previous studies (Kempinger and Christenson 1978; Schneider 1978; Hanson and Leggett 1982; Downing et al. 1990). Hanson and Leggett (1982) compiled biomass data from the literature (most from cove rotenone studies in reservoirs) ranging from 0.3 to 86 $g \cdot m^{-2}$, with the majority of values falling between roughly 2 and 40 $g \cdot m^{-2}$. Downing et al. (1990) compiled a different data set from the literature with biomass values ranging from 0.5 to 37 $g \cdot m^{-2}$. Biomass estimates from 65 lakes in Michigan ranged from 1.1 to 40.3 $g \cdot m^{-2}$, averaging 13.1 $g \cdot m^{-2}$ (Schneider 1978). Our biomass range of 6.1–26.9 $g \cdot m^{-2}$, averaging 13.5 $g \cdot m^{-2}$, corresponded well with these literature values. The literature values outside our range could reflect a variety of factors, including reduced whole-lake biomass in comparison with our biomass data derived from the littoral zone, a wider range in lake productivity and other environmental variables, larger sample size, and differences in sampling efficiency.

To our knowledge, Boisclair and Leggett (1989c) have conducted the only previous quantitative fish sampling in our 10 study lakes. Using similar methods, but sampling only during one year and without making corrections for differential capture efficiency, they obtained biomass estimates that averaged 68% of our estimates. Our use of efficiency corrections probably accounts for some of this discrepancy. Although our average biomass estimates were higher than those of Boisclair and Leggett (1989c), we found a very similar pattern of relative biomass across the 10 lakes ($r_s = 0.79$, $P = 0.006$). This comparison suggests that, despite asynchronous temporal variation, our quantitative littoral seining did reveal a repeatable pattern in relative fish biomass among lakes.

Although significant interactions involving all three main effects occurred in our analyses of variation in fish biomass, lake and seasonal effects appeared to dominate (Fig. 2; Table 3). This further indicates that there were real differences in biomass among lakes, but also suggests that samples stratified over seasons were important for accurately estimating mean biomass in lakes. For example, had only the early season samples been taken, biomass estimates in Lakes Magog and Memphremagog would be considerably higher than our current values (Fig. 2). Likewise, biomass in Lakes Brompton, Bromont, and Roxton would be much lower than current estimates. The relatively weaker year effects suggest that stratifying sampling over more than one year might be less important than sampling seasonally within a single year if the primary goal is to make comparisons among lakes. However, the relatively short time scale of our study (2 yr) limits this interpretation. Long-term fluctuations in biomass are well known (Johannes et al. 1989; Lyons 1989; Townsend 1989; Mills and Hurley 1990) and should be addressed when possible.

PCA ordination of the lakes based on mean biomass of the eight most widely distributed species resulted in a general scattering of lakes, with little tendency toward aggregation, or "clumping", into similar community types (Fig. 3). Lakes Bromont and Waterloo were perhaps the most widely separated, both having high biomass of the benthic species white sucker and brown bullhead. Lake Magog was also somewhat separated from the other lakes, having the highest total biomass. The lack of distinct littoral fish community types in these lakes may have resulted for several reasons. Our study lakes were not widely separated geographically; the greatest distance between any two lakes is approximately 110 km (Fig. 1). Studies documenting distinct fish communities often cover larger spatial scales (Jackson and Harvey 1989; Tonn et al. 1990). None of our study lakes experience winterkill, low pH, or other severe forms of environmental stress that have been shown to produce distinct fish communities (Tonn and Magnuson 1982; Rahel and Magnuson 1983). Additionally, our use of quantitative biomass data rather than the more commonly used presence/absence data may have resulted in a more diffuse ordination of communities than in other studies.

Using relative abundance data, Hinch et al. (1991) have recently presented a similarly diffuse ordination of fish communities in a series of 25 central Ontario lakes. With a slightly different mix of dominant species, they found strong negative correlations in relative abundance of white sucker and rock bass (*Ambloplites rupestris*), and brown bullhead and smallmouth bass. White sucker were more numerous in lakes without piscivorous northern pike. These distributional patterns appeared to be primarily the result of differential habitat conditions, colonization histories, and possibly predation in the case of the northern pike/white sucker pattern. Our data suggested none of these relationships. Presumably, differences in environmental conditions, zoogeographic history, differences in sampling and analytical methodology, as well as the spatial scale of sampling account for these differences. Our southern Quebec lakes are in closer proximity and contained largely sympatric populations. The relationships described by Hinch et al. (1991) were the result of allopatric distributional patterns in the Ontario lakes and disappeared when only sympatric populations were considered.

Another potential explanation for the diffuse littoral fish community pattern could be the corresponding lack of aggregation of limnological and prey resource conditions among lakes (Fig. 4). Although these ordinations provided no basis for grouping the lakes into types, they did help identify some potentially important relationships of the littoral fish communities with environmental factors. Lake size, as described by principal component Limn 1, was positively correlated with species richness (Fig. 5), as discussed above. Lakes with chironomid-dominated littoral invertebrate prey communities (Prey 2) tended to have abundant yellow perch and golden shiner (Fish 1) (Fig. 7). This relationship suggested the positive correlation of chironomid biomass with total fish biomass (Fig. 8).

Empirical relationships of fish abundance, such as the one described above, have been very useful in generating testable hypotheses and providing working models for both management and further study in aquatic systems (Rigler 1982; Peters 1986, 1991). Existing models relate production, yield, or biomass to a variety of factors such as mean depth (Rawson 1952), morphoedaphic index (Ryder 1982), nutrient concentration (Hanson and Leggett 1982; Quiros 1990), primary productivity (Oglesby 1977; Downing et al. 1990), and benthos (Matuszek 1978; Hanson and Leggett 1982). In the majority of these models, predictor variables are considered to be generalized correlates of food availability, which is usually held to be the causal factor (Ney 1990), but is difficult to accurately assess (Boisclair and Leggett 1985). Our relationship of total fish biomass with chironomid biomass, which represented 24% of the overall littoral invertebrate biomass and the most abundant nonshelled group, may reflect such a causal relationship. Chironomids are widely known to be important in the diets of several fish species (Keast and Webb 1966; Sadzikowski and Wallace 1976). Previous work in our lakes indicated that chironomids were the only prey taxon to occur in the diets of all size classes of yellow perch examined and accounted for 27% of the diet (by weight) overall, the largest percentage of any prey taxon (Boisclair and Leggett 1989b). We are currently analyzing diets and consumption rates of the other two dominant species, golden shiner and pumpkinseed, in these lakes.

The lack of significant relationships of littoral fish biomass with measures of lake productivity and total benthos biomass may have several causes. Total measured prey biomass, or correlates such as productivity, may not reflect true availability of prey to fish (Boisclair and Leggett 1985). Differential vulnerability of prey taxa as well as food preferences among predators (Stein 1979; Zaret 1980; Peckarsky 1982; Pierce 1988) may complicate such relationships. Alternatively, responses of fish biomass in the littoral zone may be obscured by shoaling, offshore migrations, habitat heterogeneity, patchy distribution of prey, and other factors (Hall and Werner 1977; Keast and Harker 1977; Helfman 1978). Combining intensive littoral sampling such as ours with estimates of intrusion into nearby pelagic areas would be necessary to evaluate this possibility. An additional explanation might be that fish respond to environmental variation and food resource availability differently in different lakes, showing various combinations of growth, production, and biomass responses. Indeed, growth of yellow perch is highly variable among these lakes (Boisclair and Leggett 1989a, 1989b, 1989c), and preliminary data indicate similarly large differences in growth of golden shiner and pumpkinseed among the lakes (unpublished data). Clearly, relationships of littoral fish communities with the suite of limnological conditions, both biotic and abiotic, as well as the suite of prey resources available are necessarily complex. In addition to the analyses of community structure and biomass presented here, it is evident that evaluations of food resource utilization, growth, and production will be required to fully characterize links between the littoral fishes and their environment. We are currently exploring these relationships.

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References

ANDERSON, M.R., AND J. KALFF. 1988. Submerged aquatic macrophyte biomass in relation to sediment characteristics in ten temperate lakes. Freshwater Biol. 19: 115–121.

BAYLEY, P.B. 1985. Sampling problems in freshwater fisheries, p. 3–13. *In* K. O'Hara, C. Aprahamian, and R.T. Leah [ed.] Proc. 4th Br. Freshwater Fish. Conf., University of Liverpool, Liverpool, U.K.

BOISCLAIR, D., AND W.C. LEGGETT. 1985. Rates of food exploitation by littoral fishes in a mesotrophic north-temperate lake. Can. J. Fish. Aquat. Sci. 42: 556–566.

BOISCLAIR, D., AND W.C. LEGGETT. 1989a. Among-population variability of fish growth: I. Influence of the quantity of food consumed. Can. J. Fish. Aquat. Sci. 46: 457–467.

BOISCLAIR, D., AND W.C. LEGGETT. 1989b. Among-population variability of fish growth: II. Influence of prey type. Can. J. Fish. Aquat. Sci. 46: 468–482.

BOISCLAIR, D., AND W.C. LEGGETT. 1989c. Among-population variability of fish growth: III. Influence of fish community. Can. J. Fish. Aquat. Sci. 46: 1539–1550.

CARLANDER, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State University Press, Ames, Iowa. 752 p.

CATTANEO, A. 1987. Periphyton in lakes of different trophy. Can. J. Fish. Aquat. Sci. 44: 296–303.

CHAMBERS, P.A., AND J. KALFF. 1985. Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701–709.

CULVER, D.A., M.M. BOUCHERLE, D.J. BEAN, AND J.W. FLETCHER. 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. Can. J. Fish. Aquat. Sci. 42: 1380–1390.

DOWNING, J.A., C. PLANTE, AND S. LALONDE. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47: 1929–1936.

DUARTE, C.M., AND J. KALFF. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. 31: 1072–1080.

DUMONT, H.J., I. VAN DE VELDE, AND S. DUMONT. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia (Berl.) 19: 75–97.

EADIE, J.MCA., AND A. KEAST. 1984. Resource heterogeneity and fish species diversity in lakes. Can. J. Zool. 62: 1689–1695.

ELLIOTT, J.M. 1988. Growth, size, biomass and production in contrasting populations of trout *Salmo trutta* in two Lake District streams. J. Anim. Ecol. 57: 49–60.

EVANS, D.O., B.A. HENDERSON, N.J. BAX, T.R. MARSHALL, R.T. OGLESBY, AND W.J. CHRISTIE. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 448–470.

FROST, T.M., D.L. DEANGELIS, S.M. BARTELL, D.J. HALL, AND S.H. HURLBERT. 1988. Scale in the design and interpretation of aquatic community research. *In* S.R. Carpenter [ed.] Complex interactions in lake communities. Springer-Verlag, New York, N.Y.

HALL, D.J., AND E.E. WERNER. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Trans. Am. Fish. Soc. 106: 545–555.

HANEY, J.F., AND D.J. HALL. 1973. Sugar-coated *Daphia*: a preservation technique for Cladocera. Limnol. Oceanogr. 18: 331–333.

HANSON, J.M., AND W.C. LEGGETT. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39: 257–263.

HELFMAN, G.S. 1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fishes 3: 129–148.

HINCH, S.G. 1991. Small- and large-scale studies in fisheries ecology: the need for cooperation among researchers. Fisheries 16(3): 22–27.

HINCH, S.G., N.C. COLLINS, AND H.H. HARVEY. 1991. Relative abundance of littoral zone fishes: biotic interactions, abiotic factors, and postglacial colonization. Ecology 72: 1314–1324.

JACKSON, D.A., AND H.H. HARVEY. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. Ecology 70: 1472–1484.

JOHANNES, M.R.S., D.J. MCQUEEN, T.J. STEWART, AND J.R. POST. 1989. Golden shiner (*Notemigonus crysoleucas*) population abundance: correlations with food and predators. Can. J. Fish. Aquat. Sci. 46: 810–817.

KEAST, A., AND J. HARKER. 1977. Fish distribution and benthic invertebrate biomass relative to depth in an Ontario lake. Environ. Biol. Fishes 2: 235–240.

KEAST, A., AND D. WEBB. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845–1874.

KEMPINGER, J.J., AND L.M. CHRISTENSON. 1978. Population estimates and standing crops of fish in Nebish Lake. Wis. Dep. Nat. Resour. Res. Rep. 96: 12 p.

KERR, S.R., AND R.A. RYDER. 1988. The applicability of fish yield indices in freshwater and marine ecosystems. Limnol. Oceanogr. 33: 973–981.

LYONS, J. 1987. Distribution, abundance, and mortality of small littoral-zone fishes in Sparkling Lake, Wisconsin. Environ. Biol. Fishes 18: 93–107.

LYONS, J. 1989. Changes in the abundance of small littoral-zone fishes in Lake Mendota, Wisconsin. Can. J. Zool. 67: 2910–2916.

LYONS, J., AND J.J. MAGNUSON. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Trans. Am. Fish. Soc. 116: 29–39.

MARSHALL, T.R., AND P.A. RYAN. 1987. Abundance patterns and community attributes of fishes relative to environmental gradients. Can. J. Fish. Aquat. Sci. 33(Suppl. 2): 198–215.

MATUSZEK, J.E. 1978. Empirical predictions of fish yields of large North American lakes. Trans. Am. Fish. Soc. 107: 385–394.

MATUSZEK, J.E., AND G.L. BEGGS. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

MILLS, C.A., AND M.A. HURLEY. 1990. Long-term studies on the Windemere populations of perch (*Perca fluviatilis*), pile (*Esox lucius*) and arctic charr (*Salvelinus alpinus*). Freshwater Biol. 23: 119–136.

MITTELBACH, G.G. 1986. Predator-mediated habitat use: some consequences for species interactions. Environ. Biol. Fishes 16: 159–169.

MURPHY, B.R., D.W. WILLIS, AND T.A. SPRINGER. 1991. The relative weight index in fisheries management: status and needs. Fisheries 16: 30–38.

NEY, J.J. 1990. Trophic economics in fisheries: assessment of demand–supply relationships between predators and prey. Rev. Aquat. Sci. 2: 55–81.

NORTHCOTE, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. Can. J. Fish. Aquat. Sci. 45: 361–379.

OGLESBY, R.T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production and morphoedaphic factors. J. Fish. Res. Board Can. 34: 2271–2279.

PACE, M.L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus – chlorophyll *a* relationship. Can. J. Fish. Aquat. Sci. 41: 1089–1096.

PACE, M.L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. Limnol. Oceanogr. 31: 45–55.

PECKARSKY, B.L. 1982. Aquatic insect predator–prey relations. BioScience 32: 261–266.

PETERS, R.H. 1986. The role of prediction in limnology. Limnol. Oceanogr. 31: 1143–1159.

PETERS, R.H. 1991. A critique for ecology. Cambridge University Press, Cambridge, U.K. 366 p.

PIERCE, C.L. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. Oecologia (Berl.) 77: 81–90.

PIERCE, C.L., J.B. RASMUSSEN, AND W.C. LEGGETT. 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. Can. J. Fish. Aquat. Sci. 47: 1004–1010.

QUIROS, R. 1990. Predictors of relative fish biomass in lakes and reservoirs of Argentina. Can. J. Fish. Aquat. Sci. 47: 928–939.

RAHEL, F.J. 1986. Biogeographic influences on fish species composition of northern Wisconsin lakes with applications for lake acidification studies. Can. J. Fish. Aquat. Sci. 43: 124–134.

RAHEL, F.J., AND J.J. MAGNUSON. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural eutrophication. Can. J. Fish. Aquat. Sci. 40: 3–9.

RASMUSSEN, J.B. 1988a. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. Can. J. Fish. Aquat. Sci. 45: 1436–1447.

RASMUSSEN, J.B. 1988b. Habitat requirements of burrowing mayflies (Ephemeridae: *Hexagenia*) in lakes, with special reference to the effects of eutrophication. J. N. Am. Benthol. Soc. 7: 51–64.

RASMUSSEN, J.B. 1993. Patterns in the size structure of littoral zone macroinvertebrate communities. Can. J. Fish. Aquat. Sci. 50: 2192–2207.

RAWSON, D.S. 1952. Mean depth and the fish production of large lakes. Ecology 33: 513–521.

RIGLER, F.H. 1982. Recognition of the possible: an advantage of empiricism in ecology. Can. J. Fish. Aquat. Sci. 39: 1323–1331.

ROWAN, D.J., J. KALFF, AND J.D. RASMUSSEN. 1992. Profundal sediment organic content and physical character do not reflect lake trophic status, but rather reflect inorganic sedimentation and exposure. Can. J. Fish. Aquat. Sci. 49: 1431–1438.

RYDER, R.A. 1982. The morphoedaphic index — use, abuse, and fundamental concepts. Trans. Am. Fish. Soc. 111: 154–164.

SADZIKOWSKI, M.R., AND D.C. WALLACE. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus*, *L. gibbosus* and *L. cyanellus*). Am. Midl. Nat. 95: 220–225.

SAS INSTITUTE INC. 1988. SAS/STAT user's guide. Release 6.03 edition. SAS Institute Inc., Cary, N.C. 1028 p.

SCHNEIDER, J.C. 1978. Predicting the standing crop of fish in Michigan lakes. Mich. Dep. Nat. Resour. Fish. Res. Rep. 1860: 10 p.

SCHNEIDER, J.C. 1981. Fish communities in warmwater lakes. Mich. Dep. Nat. Resour. Fish. Res. Rep. 1860: 22 p.

SMOCK, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. 10: 375–381.

STEIN, R.A. 1979. Behavioral response of prey to fish predators, p. 343–353. *In* R.H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

STRICKLAND, J.D.H., AND T.R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Board Can. 167: 310 p.

TONN, W.M., AND J.J. MAGNUSON. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63: 1149–1166.

TONN, W.M., J.J. MAGNUSON, M. RASK, AND J. TOIVONEN. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. Am. Nat. 136: 345–375.

TOWNSEND. C.R. 1989. Population cycles in freshwater fish. J. Fish Biol. 35: 125–131.

UNDERHILL, J.C. 1986. The fish fauna of the Laurentian Great Lakes, the St. Lawrence Lowlands, Newfoundland and Labrador, p. 105–136. *In* C.H. Hocutt and E.O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, N.Y.

WATERS, T.F. 1982. Annual production by a stream brook charr population and by its principal invertebrate food. Environ. Biol. Fishes 7: 165–170.

WELLS, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954–75. J. Fish. Res. Board Can. 34: 1821–1829.

WERNER, E.E., D.J. HALL, D.R. LAUGHLIN, D.J. WAGNER, L.A. WILSMANN, AND F.C. FUNK. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360–370.

WOOTTON, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London, U.K. 404 p.

ZARET, T.M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Conn. 187 p.