The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages

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Abstract: Fish assemblages in small lakes (≤50 ha) in central Ontario were characterized to determine the impact of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. Data were collected employing minnow traps and visual assessment. Although species richness did not differ between lakes with and without smallmouth bass, species composition and relative abundance did differ. We identified two distinct fish assemblage types: one characterized by small-bodied species, mainly cyprinids, and a second by large-bodied centrarchid species, e.g., smallmouth bass. Smallmouth bass appear to reduce abundance, alter habitat use, and extirpate many small-bodied species such as brook stickleback (*Culaea inconstans*), fathead minnow (*Pimephales promelas*), pearl dace (*Margariscus margarita*), and *Phoxinus* spp.

Résumé : La caractérisation des peuplements de poissons du littoral de petits lacs (≤50 ha) du centre de l'Ontario a permis d'évaluer l'impact de la prédation de l'Achigan à petite bouche (*Micropterus dolomieu*) et de la complexité de l'habitat sur la structure des communautés. Les données consistaient en des récoltes faites à la nasse et des estimations visuelles. La composition spécifique des peuplements de poissons et l'abondance relative des espèces différaient entre les lacs où l'achigan était présent et ceux où il était absent, mais pas la richesse en espèces. Il a été possible de distinguer deux types de peuplements, l'un composé de poissons à corps élancé, en majorité des cyprinidés, et l'autre dominé par des poissons centrarchidés à corps massif, e.g., l'achigan. La présence de l'achigan semble donc réduire l'abondance des poissons, modifier l'utilisation de l'habitat et éliminer plusieurs des poissons à corps élancé, tels que l'Épinoche à cinq épines (*Culaea inconstans*), le Tête-de-boule (*Pimephales promelas*), le Mulet perlé (*Margariscus margarita*) et les *Phoxinus* spp.

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Introduction

Human-induced environmental disturbances have led to the alteration of species distributions around the world. Concern about the introduction of nonnative species into aquatic ecosystems has led to a growing concern regarding the loss of native fish biodiversity (Chapleau et al. 1997). Most fish introductions, whether intentional or unintentional, have negative effects on native fishes and other taxa through predation, competition, hybridization, and introduction of diseases (Allendorf 1991) and possibly habitat alteration, trophic alterations, and gene pool deterioration (Crossman 1991).

Temperate lakes contain fish communities whose composition and richness are shaped by a number of biotic and abiotic factors, and piscivory appears to be one of the major factors contributing to community structure (Tonn and Magnuson 1982). Piscivores alter small-fish assemblage composition in small boreal lakes by excluding predation-intolerant species (Harvey 1981; Tonn and Magnuson 1982) among other effects. Because piscivores are size-selective and gape-limited (Tonn and Paszkowski 1986; Post and Evans 1989), small fishes are generally more vulnerable to predation than large fish (Tonn et al. 1992), although it may be a combination of size and morphology that determines risk to predation (He and Kitchell 1990. These small-bodied species could potentially be eliminated from a lake if local predators are able to eat all size classes (Tonn et al. 1992). Therefore, small-bodied species are often reduced in richness (Jackson 1988) or absent from small lakes containing littoral piscivores (Harvey 1981; Tonn and Magnuson 1982; Jackson et al. 1992). Vulnerable species vary by lake but studies have shown certain small-bodied species to be particularly susceptible to piscivorous fish predation (Jackson 1988; Naud and Magnan 1988; He and Wright 1992). Recruitment of larger-bodied species may be regulated by piscivores but these species would not likely be eliminated from lakes if adults attained a size large enough to escape predation (Tonn et al. 1992).

It is generally accepted that complex habitats are safer for prey than more open habitats (Crowder and Cooper 1982). Complex habitats provide greater amounts of refuge for fish, refuge being defined as a physical location where the prey can live or temporarily hide to live (McNair 1986). However, more open habitats can be more profitable for resources than

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Table 1. Location and surface area of Ontario lakes and presence or absence of smallmouth bass.

Lake	Location	Area (ha)	Smallmouth bass
Grindstone (GR)	45°11′N, 78°52′W	32	Present
Heron (HE)*	45°27′N, 78°49′W	24	Present
Kearney (KE)*	45°35′N, 78°27′W	32	Present
Little Wren (LWR)	45°11′N, 78°51′W	16	Present
Louie (LO)	45°23′N, 78°44′W	31	Present
Plastic (PL)	45°11′N, 78°50′W	33	Present
Wren (WR)	45°11′N, 78°42′W	50	Present
Bluff (BL)	45°35′N, 78°20′W	8	Absent
Jake (JK)	45°34′N, 78°33′W	6	Absent
Marmot (MR)	45°41′N, 78°24′W	3	Absent
Poorhouse (PRH)	45°22′N, 78°45′W	30	Absent
Scott (SC)	45°29′N, 78°43′W	28	Absent
Sproule (SP)*	45°36′N, 78°23′W	43	Absent
Sunday (SU)*	45°36′N, 78°21′W	46	Absent

Note: Sampling dates include cycle 1 (May 15–18), cycle 2 (May 21–26), cycle 3 (June 7–18), cycle 4 (June 28 – July 10), cycle 5 (summer survey, July 26 – August 21), and cycle 6 (September 9–13).

*Sampled repeatedly throughout the course of the summer.

complex habitats (Werner et al. 1983). The trade-off between resource availability and predation risk determines the habitat use patterns of fish (Mittlebach 1981; Werner et al. 1981; Crowder and Cooper 1982), and species have been shown to reduce the risk of predation by finding refuge at the expense of foraging efficiency (Phelan and Baker 1992).

Piscivorous fishes have the ability to influence the distribution of their prey, which may alter the feeding habits of the prey by constraining their feeding space or time, preventing their colonization of habitats or causing them to emigrate, which all may ultimately reduce their numbers (Power et al. 1985; Jackson et al. 2001). Tonn and Magnuson (1982) describe the distinction of lakes dominated by large piscivores verses Umbra-cyprinid species, where the small bodied species were either rare or absent from lakes with large piscivores. Many fish populations have been eliminated, in large part, because of predation (Zaret and Paine 1973).

Knowing the importance of complex habitat as refuge, we recognize the need to protect these fish habitats. However, with the continued development of lakes, there is an increasing trend to remove important fish habitat components such as woody debris and macrophytes. Lake development is coupled with the alteration of shoreline fish habitat. Developed lakes, those lakes influenced by human land use, have less woody habitat than undeveloped lakes (Christensen et al. 1996). Bryan and Scarnecchia (1992) compared developed and undeveloped lakes and found fish richness and abundance to be greater in undeveloped lakes, which contained a greater proportion of complex vegetation structure. Lakes undergoing shoreline development are the same lakes with high fishing pressure, making them particularly susceptible to sport fish introductions due to the increase in accessibility of the lake (Jackson et al. 2001). As well, piscivores have been demonstrated to prosper in some developed habitats. Bryan and Scarnecchia (1992) discovered that smallmouth bass (*Micropterus dolomieu*) were more abundant in developed lakes compared with undeveloped lakes. Yet species, largely game species, are often introduced into lakes with little regard to their impact aside from their recreational opportunities.

In this study, we investigated the long-term impact of piscivorous fish on the littoral fish community structure of small temperate lakes. There is a long history of smallmouth bass introductions into Ontario lakes, although they are not well documented. Smallmouth bass were introduced into lakes in Algonquin Provincial Park, Ontario, beginning in the early 1900s (Christie 1957) and have been introduced into other lakes to supplement the sport fishery for native salmonids (Ridgway et al. 1991). From these initial introductions, natural colonization of watersheds has occurred. As a result of the continued introduction of smallmouth bass, concern is being raised regarding the potential impact that they may have on indigenous species. In the absence of pre-introduction fish community data, lakes lacking piscivores can be used to assess the impact of smallmouth bass introductions on native fish communities (Chapleau et al. 1997).

We sought to quantify the long-term impact of smallmouth bass on fish community structure by asking the following questions. Does total species richness and abundance of littoral fishes differ between lakes with and without smallmouth bass? What effect do smallmouth bass have on the use of complex and simple habitats by species vulnerable to smallmouth bass predation? Does a difference exist in the size of species vulnerable to predation between complex habitats offering refuge and those habitats of simple, more open areas in lakes with and without smallmouth bass?

Methods

Study design

This project comprised two studies. One was an intensive examination of fish assemblages in four lakes during May to September using visual assessment and trapping techniques to identify and count fish. The second, a study of 14 lakes sampled during maximum summer water temperatures, was a broader study with less intensive sampling but a larger number of lakes. Lakes chosen for this study were all ≤50 ha (mean surface area of 31 ha for lakes with smallmouth bass and 26.3 ha for lakes without smallmouth bass); secluded lakes were preferred to reduce tampering with sampling gear and other sources of disturbance by the public. Lakes chosen were divided into two groups: lakes with smallmouth bass, an introduced littoral piscivorous predator, and lakes without smallmouth bass. The dates of smallmouth bass introduction or colonization are unknown and varied among lakes.

Four lakes were sampled for fish during May through September 1998. Each lake was sampled on six different occasions, referred to as the sampling cycles (Table 1). This portion of the project was designated the “base study.” In the larger study, 14 lakes (Table 1) were sampled for fish during mid-July through mid-August (Table 2) and designated the “summer survey.” These lakes were sampled only once to increase sample size. Base study results revealed that the combination of trap and visual data for 1 day of sampling is representative of a littoral fish community (MacRae 1999). In the base study, an initial shoreline cruise was done to record relative habitat complexity of the littoral zone. Six sites were chosen per lake, three complex habitats and three simple habitats to maximize the habitat contrast. The design was to contrast habitat types with high complexity offering fish refuge versus low-complexity or simple sites offering little to no cover available to fish in order to

Table 2. Presence (1) – absence (empty cell) data from the combined sampling using minnow traps and visual sampling from Ontario lakes.

	Lakes with smallmouth bass							Lakes without smallmouth bass						
Species	GR	LO	WR	PL	LWR	HE	KE	SU	SP	PRH	JK	BL	MR	SC
Rock bass (RB)		1	1	1	1									
Largemouth bass (LMB)			1		1									
Smallmouth bass (SMB)	1	1	1	*	1	1	1							
Yellow perch (YP)	1	1	1	1	1	1	1	1	1					
Common shiner (CS)			1		1	1	1	1	1					
Bluntnose minnow (BNM)		1			1	1	1			1				
Pumpkinseed (PS)	1	1	1	1	1	1	1	1		1	1			
Brown bullhead (BBH)					1			1						
Blacknose shiner (BNS)						1	1	1	1	1				
Creek chub (CC)		1		1	1	1	1	1	1	1	1			
Pearl dace (PD)								1	1					
Iowa darter (ID)									1					
White sucker (WS)						1	1		1			1		
Golden shiner (GS)			1		1		1		1	1	1	1	1	
Phoxinus spp. (PH)								1	1	1	1	1	1	1
Brook stickleback (BRS)										1	1	1		1
Fathead minnow (FHM)										1	1	1	1	1
Brook trout		*				*	*	*	*	*	*		*	*
Lake trout		*	*		*	*	*	*						*
Splake								*	*					*
Burbot			*		*	*	*	*						

Note: Lakes and species are ordered as they appear along the first axis in the correspondence analysis (Fig. 1) to show the pattern in species assemblages. See Table 1 for lake name abbreviations.
*Piscivorous species previously found in the lake (e.g., Jackson 1988) but not captured during this study.

identify whether there are differences in habitat use by fish in the presence and absence of smallmouth bass. Complex habitats had high quantities of coarse, large woody material and (or) vegetation. Simple habitats were composed mainly of sand, gravel, rocks, and boulders, with little to no wood or vegetation. Although the degree of complexity within either category may vary across the lakes, the within-lake contrast is the relevant level of comparison. Sites were selected as evenly distributed around the lake as possible within the habitat designations. To maintain independence of sampling areas, areas were at least 60 m from one another. Visual sampling and trapping were conducted within each of the chosen sites. This methodology resulted in a stratified, randomized design (McInerny and Degan 1993; Whittier and Hughes 1998). Through the summer survey, all sites sampled visually and by trapping were randomly chosen. Visual sampling was completed throughout the entire shoreline in small lakes (≤6 ha).

Sampling protocol

All sites within lakes were swum using snorkeling gear to record presence–absence data of fish species. A total of ten 5-m transects were set 1–1.5 m from shore at a depth of 1–2.5 m at each site selected to ensure that species that may not be caught in minnow traps due to species selectivity and bias would be included in the presence–absence data. Lakes were then sampled with 18 baited minnow traps to assess the relative abundance of the fish assemblage. These were commercially available Gee minnow traps with an opening diameter of 2–3 cm. Traps were baited with a dry cereal based dog kibble and were set near the shoreline at depths ranging from 0.5 to 2 m. Traps were set over night and collected in the morning, after about 16 h of sampling. Fish collected were counted and identified to species (Table 2). Minnow traps were shown to provide a good estimate of the littoral fish communities based on comparisons with other sampling protocols and known community composition (MacRae 1999). Subsamples of a maximum of 25 individuals of each species were chosen as encountered and total length was measured. Only small-bodied species, e.g., cyprinids, and the young of larger species were collected in minnow traps due to size selection of traps. However, it is these small species, as well as the young-of the-year from other larger-bodied species, that are most vulnerable to smallmouth bass predation.

Statistical analysis

Relative abundance estimates of fish data were derived from mean catch per unit effort (XCPUE) of fish collected from minnow traps. XCPUE estimates of species relative abundance were compared for each species between lakes with and without smallmouth bass, and length of fish and mean total length per species were compared between habitat types. Comparisons employed a t test assuming unequal variance. A one-way test was employed for vulnerable species because an assumption of distribution was apparent, while all other species were compared using a two-way distribution test. Combined results from individual species comparisons were tested using the combined probabilities test (Sokal and Rohlf 1995) and a binomial test of trends in species abundance between habitats.

Correspondence analysis (e.g., Jackson and Harvey 1989) was used to summarize the underlying composition of fish communities and lake similarity and to graphically demonstrate the separation of species–lake relationships characterized in this study. Species and lakes positioned in similar ordination space represent species–lake associations that occur together more frequently than would be expected if species were randomly distributed across the lakes. Correspondence analysis results are presented for the summer survey using presence–absence data and relative abundance estimates (XCPUE). Species caught or observed only once in a single lake were excluded.

Results

Eighteen species were sampled from these lakes during the base study and summer survey combined and include

Table 3. Comparison of fish abundance estimates (mean catch per unit effort (XCPUE)) between lakes with and without smallmouth bass in the summer survey.

	XCPUE				
Species	Lakes with smallmouth bass	Lakes without smallmouth bass	Difference	Probability	Trend
Blacknose shiner	0.01	0.04	–0.03	0.08	Negative
Bluntnose minnow	0.49	3.73	–3.33	0.20	Negative
Brook stickleback	0	0.31	–0.31	0.08	Negative
Fathead minnow	0	38.15	–38.15	0.01	Negative
Pearl dace	0	0.08	–0.08	0.15	Negative
Phoxinus spp.	0	38.64	–38.64	0.03	Negative
Brown bullhead	0	0.01	–0.01	0.36	Negative
Common shiner	0.18	0.08	0.10	0.59	Positive
Creek chub	1.10	1.20	–0.10	0.91	Negative
Golden shiner	0.08	1.59	–1.50	0.11	Negative
Largemouth bass	0.01	0	0.01	0.36	Positive
Pumpkinseed	4.76	1.02	3.73	0.05	Positive
Rock bass	0.82	0	0.82	0.09	Positive
Smallmouth bass	0.06	0	0.06	0.07	Positive
White sucker	0	0.14	–0.14	0.29	Negative
Yellow perch	0.53	0.28	0.25	0.38	Positive

Note: "Difference" category is the difference between the mean abundance values per minnow trap for the lakes with smallmouth bass minus the mean abundance values for the lakes without smallmouth bass. The probability value is for the associated *t* test.

those species caught in minnow traps or observed in visual samples. Brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), and splake (*S. fontinalis* × *S. namaycush*) have been captured in these lakes in previous studies using other types of sampling gear (Table 2). These salmonids inhabit cool or cold water during the summer months and would not be expected in the warm littoral zone due to high temperature. Two species occurred in only one lake; burbot (*Lota lota*) and Iowa darter (*Etheostoma exile*) were found in Sproule Lake. Largemouth bass (*Micropterus salmoides*) was found in only two lakes, Wren Lake and Little Wren Lake, that are connected by a short watercourse. Only young-of-the-year were found in both lakes, and largemouth bass were not found during previous surveys (Jackson 1988) but were known to be in nearby lakes. They may have colonized or been introduced into these two lakes since that sampling.

In the base study, species richness did not differ between lakes with and without smallmouth bass. However, reductions in abundance or the absence of small-bodied species, including blacknose shiner (*Notropis heterolepis*), bluntnose minnow (*Pimephales notatus*), pearl dace (*Margariscus margarita*), and *Phoxinus* spp. (northern redbelly dace (*Phoxinus eos*) and (or) finescale dace (*Phoxinus neogaeus*)), were observed in lakes with smallmouth bass. Abundance estimates for fish between base study lakes or habitat types were not compared statistically due to low sample size (four lakes). From the 14 lakes sampled in July through August, no significant difference in species richness between lakes with and without smallmouth bass was observed (Mann–Whitney $U = 22$, $p = 0.75$). However, species most vulnerable to predation were absent from lakes with smallmouth bass. Species absent or lower in abundance in lakes with smallmouth bass include the fathead minnow (*Pimephales promelas*) ($p = 0.01$), *Phoxinus* spp. ($p = 0.03$), brook stickleback (*Culaea inconstans*) ($p = 0.08$), and blacknose shiner ($p = 0.09$) (Table 3). An overall significance test showed a greater abundance of vulnerable species in lakes without smallmouth bass ($\chi^2_{12} = 33.31$, $p = 0.001$; binomial distribution test (BNMDT), $p = 0.01$) (Table 4*a*) relative to those lakes with smallmouth bass. A comparison of all other species in lakes showed mostly increased but nonsignificant trends in species abundance in smallmouth bass lakes compared with those lakes without smallmouth bass (Table 3). Overall significance tests indicated no difference in these species abundances between lakes with and without smallmouth bass ($\chi^2_{20} = 30.47$, $p = 0.63$; BNMDT, $p = 0.20$) (Table 4*a*). Although species richness did not differ between lakes with and without smallmouth bass, their species compositions were distinct. Lakes with smallmouth bass contained 2.3 fewer small-bodied species, on average, than lakes without smallmouth bass.

Results did not reveal significant differences in species abundance between habitat types; however, comparisons of abundance estimates between habitat types showed a greater abundance of vulnerable species in complex over simple habitats where subject to smallmouth bass predation. While no significant difference in abundance of fish between habitats was found ($\chi^2_4 = 5.70$, $p = 0.22$; BNMDT, $p = 0.25$; nonsignificance is due to low sample size (n = 2)) (Table 4*b*), low sample size and statistical power is due to the fact that four of the six vulnerable species, brook stickleback, fathead minnow, pearl dace, and *Phoxinus* spp., were absent from all summer survey lakes containing smallmouth bass. This situation results from these species often being unable to persist in lakes with smallmouth bass; however, not all lakes without bass contain all of these small-bodied species. Most other species also showed a trend of greater abundance in complex over simple habitats in lakes with smallmouth bass (Table 5). The overall test of significance showed a preference of complex habitats ($\chi^2_{12} = 26.05$, $p = 0.053$; BNMDT, $p = 0.03$), indicating a greater abundance of

Table 4. Overall tests of significance (χ^2 and binomial test) for differences (*a*) in relative abundance between lakes with and without smallmouth bass, (*b*) in relative abundance between habitats for both vulnerable species and all other species, (*c*) in total length of species between habitats in the base lakes, and (*d*) in total length of species between habitats in lakes with and without smallmouth bass.

	Observed χ^2 value	Critical χ^2 value	Associated probability	Binomial probability
(*a*) Relative abundance in lakes with smallmouth bass versus lakes without smallmouth bass				
Vulnerable species	33.31		0.001	0.01
Other species	30.47		0.63	0.21
(*b*) Relative abundance between habitats in lakes with smallmouth bass versus lakes without smallmouth bass				
Vulnerable species				
Bass: complex versus simple habitat	5.70		0.22	0.25
No bass: complex versus simple habitat	20.95		0.05	0.09
Other species				
Bass: complex versus simple habitat	26.05		0.05	0.03
No bass: complex versus simple habitat	16.31		0.29	0.27
(*c*) Differences in length of fish between simple and complex habitats in base lakes				
Heron Lake	6.25		0.9	0.31
Kearney Lake	12.01		0.44	0.23
Sunday Lake	22.97		0.29	0.21
Sproule Lake	7.87		0.89	0.27
(*d*) Differences in length of fish between lakes with smallmouth bass versus lakes without smallmouth bass in the summer survey				
Bass	11.57	21.02	0.48	0.09
No bass	5.81	28.86	0.99	0.16

nonvulnerable species in complex habitats relative to simple habitats in lakes with smallmouth bass.

A comparison of abundance estimates between complex and simple habitats in lakes without smallmouth bass showed reduced abundance of vulnerable species in the complex habitats (Table 5). Combined probability and binomial distribution tests reveal a greater abundance of vulnerable species in simple habitats (χ^2_{18} = 20.95, p = 0.051; BNMDT, p = 0.09). All other species showed no trend in habitat preference in lakes when smallmouth bass were not present (χ^2_{20} = 16.31, p = 0.295; BNMDT, p = 0.27).

Length data

Minnow traps are size selective given their limited size of the opening; however, those species considered vulnerable to smallmouth bass predation would not be limited by the trap's opening. No clear trends existed in the size of these fish in the two habitats of the lakes with and without smallmouth bass in the base study. Overall, significance tests revealed that total length of fish, mean total length per species across species, did not differ between habitats in lakes with and without smallmouth bass (Heron Lake: χ^2_{12} = 6.25, p = 0.90; BNMDT, p = 0.31; Kearney Lake: χ^2_{12} = 12.01, p = 0.44; BNMDT, p = 0.23; Sproule Lake: χ^2_{14} = 7.87, p = 0.89; BNMDT, p = 0.27; Sunday Lake: χ^2_{20} = 22.97, p = 0.29; BNMDT, p = 0.21) (Table 4*c*). The summer survey revealed no trend for total length of species in the two habitats in lakes subject to smallmouth bass predation (χ^2_{12} = 11.57, p = 0.48; BNMDT, p = 0.09) (Table 4*d*). There was no significant difference in total length of all species between habitats in lakes without smallmouth bass (χ^2_{22} = 5.81, p = 0.99; BNMDT, p = 0.16).

Species–lake relationships

Presence–absence data

Correspondence analysis revealed a separation of lakes with and without smallmouth bass along the first axis (Fig. 1). Base lakes, Sproule Lake and Sunday Lake, were together and were separated from other lakes along the first and second axis by rare species (brown bullhead (*Ameiurus nebulosus*), Iowa darter, and pearl dace). Lakes with smallmouth bass were positioned at coordinates similar to the larger centrarchid species, whereas lakes without smallmouth bass were closely associated with small-bodied species, mainly cyprinids and brook stickleback (Fig. 1). Species close to the origin (e.g., common shiner (*Luxilus cornutus*), creek chub (*Semotilus atromaculatus*), pumpkinseed (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*)) were common species and (or) were found in most lakes regardless of the presence or absence of smallmouth bass. Species positioned at the far left end of axis 1 (e.g., brook stickleback, fathead minnow, *Phoxinus* spp.) were found frequently in the same lakes. This group of species was positioned separately from the group containing smallmouth bass, largemouth bass, and rock bass (*Ambloplites rupestris*), indicating that these two groups of species were not found in the same lakes. Blacknose shiner and bluntnose minnow were positioned between lakes with and without smallmouth bass and showed little affinity towards being in lakes either with or without smallmouth bass.

Relative abundance data (XCPUE)

Correspondence analysis employing XCPUE data showed results similar to those of the presence–absence plot. Lakes with and without smallmouth bass were separated along the first axis (Fig. 2). Sproule Lake and Sunday Lake were positioned closer to Heron Lake and Kearney Lake, base lakes with smallmouth bass, due to high trap catches of blacknose shiner and common shiner in all of these lakes. Larger centrarchids were grouped together as were the lakes containing them, whereas small-bodied and rare species were associated with lakes without smallmouth bass. Four groups of species were identified. The first, mainly cyprinids, was associated with lakes without smallmouth bass and was

Table 5. Comparison of fish relative abundance estimates (mean catch per unit effort (XCPUE)) between complex and simple habitats during the summer survey period.

Species	XCPUE		Difference	Associated probability	Trend
	Complex habitat	Simple habitat			
Lakes with smallmouth bass					
Blacknose shiner	0.01	0	0.01	0.18	Positive
Bluntnose minnow	0.38	0.31	0.07	0.32	Positive
Brook stickleback	0	0	0	na	
Fathead minnow	0	0	0	na	
Pearl dace	0	0	0	na	
Phoxinus spp.	0	0	0	na	
Brown bullhead	0	0	0	na	
Common shiner	0.26	0	0.26	0.33	Positive
Creek chub	1.61	0.18	1.43	0.19	Positive
Golden shiner	0.17	0	0.17	0.13	Positive
Largemouth bass	0	0.02	–0.02	0.36	Negative
Pumpkinseed	6.42	2.98	3.44	0.02	Positive
Rock bass	0.98	0.69	0.29	0.59	Positive
Smallmouth bass	0.07	0.06	0.01	0.62	Positive
White sucker	0	0	0	na	
Yellow perch	0.82	0.11	0.71	0.71	Positive
Lakes without smallmouth bass					
Blacknose shiner	0.03	0.05	–0.02	0.37	Negative
Bluntnose minnow	2.65	3.75	–1.10	0.18	Negative
Brook stickleback	0.19	0.27	–0.08	0.25	Negative
Fathead minnow	36.56	47.68	–11.12	0.25	Negative
Pearl dace	0.03	0.13	–0.09	0.22	Negative
Phoxinus spp.	43.58	33.70	9.88	0.03	Positive
Brown bullhead	0.02	0	0.02	0.36	Positive
Common shiner	0	0.02	–0.02	0.36	Negative
Creek chub	1.06	1.43	–0.37	0.35	Negative
Golden shiner	0.85	2.19	–1.35	0.28	Negative
Largemouth bass	0	0	0	na	
Pumpkinseed	1.52	0.53	0.99	0.34	Positive
Rock bass	0	0	0	na	
Smallmouth bass	0	0	0	na	
White sucker	0.08	0.21	–0.13	0.36	Negative
Yellow perch	0.32	0.24	0.09	0.19	Positive

Note: "Difference" category is the difference between the mean abundance values per minnow trap for the complex habitat minus the mean abundance values for the simple habitat. The probability value is for the associated *t* test (one-tailed test for the vulnerable species and two-tailed test for all other species). na, not applicable.

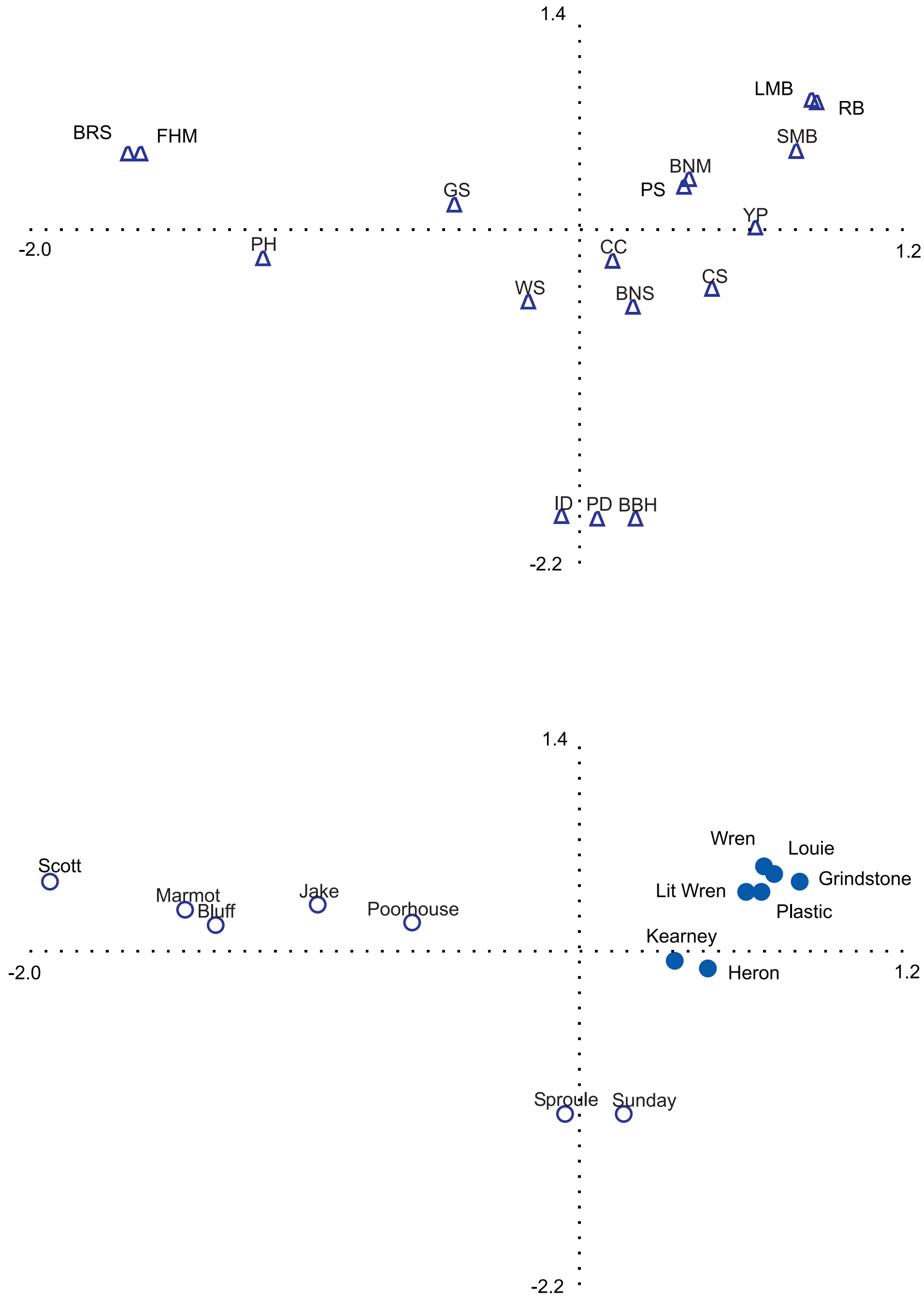
positioned at the left end of axis 1. The second group (e.g., creek chub and common shiner), a group of common species, was associated with the base lakes studied. The third group consisted of smallmouth bass and yellow perch, and the final group comprising other centrarchid species was associated with summer survey lakes containing smallmouth bass. Blacknose shiner and bluntnose minnow were positioned closer to the lakes without smallmouth bass compared with the presence–absence ordination (Fig. 1), indicating that although they were sometimes found with smallmouth bass, they were more abundant in lakes without smallmouth bass. Clearly, lakes characterized by centrarchids were separated from those with cyprinids and brook stickleback.

Discussion

An average of 5.4 fish species were found in the littoral zone and did not differ between lakes with and without piscivorous smallmouth bass. However, the fish community structure differed. Lakes with smallmouth bass had an average of 2.3 fewer small-bodied species compared with lakes without smallmouth bass. We identified two distinct fish assemblages, one characterized by a group of cyprinid species and brook stickleback and the other by large-bodied centrarchid species. The most apparent difference between the two assemblage types was the strong negative relationship between centrarchid assemblage and the brook stickleback – fathead minnow – *Phoxinus* spp. assemblage.

Piscivores alter small fish assemblage composition in small boreal lakes by excluding predation-intolerant species (Harvey 1981; Tonn and Magnuson 1982) through predation and (or) emigration of the small fish (He and Kitchell 1990). While our study showed clear separation of fish assemblage types between those lakes composed of large centrarchid species and those containing mainly small-bodied species, we also showed a trend in habitat use by small fishes in

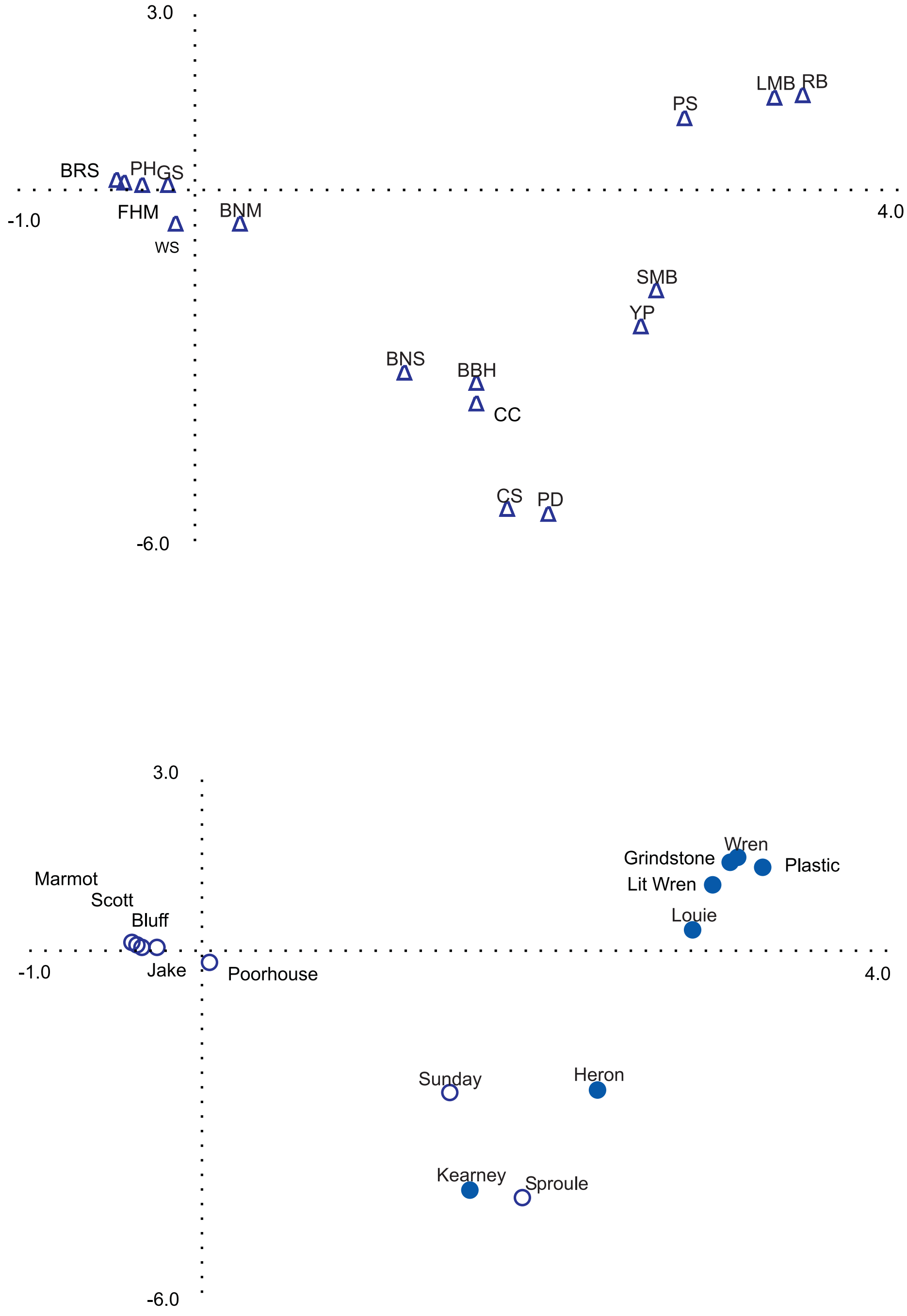
Fig. 1. Axes 1 and 2 from a correspondence analysis of species presence–absence for summer survey lakes. Solid circles identify lakes containing smallmouth bass, and open circles identify lakes without smallmouth bass. See Table 2 for species abbreviations.



these lakes where smallmouth bass were present. This distinction of lakes containing or lacking smallmouth bass is apparent, although other piscivorous species, i.e., salmonids, present in these lakes do not show such relationships with the small-bodied species. Summer thermal characteristics would separate the vulnerable species from the salmonids, thereby minimizing the predation effect during the periods of reproduction and greatest activity and growth for the small species. However, effects similar to the contrast between smallmouth bass and no smallmouth bass should be found with other strong littoral predators, e.g., northern pike (*Esox lucius*), but they were not present in these lakes. Results from our study indicate predation by smallmouth bass as being the most parsimonious explanation for the observed differences in richness of vulnerable species and overall differences in composition between lakes with and without smallmouth bass. Although these results are observational rather than manipulative, the evidence strongly supports predation as the primary factor causing the difference in the species composition in lakes. These results are comparable with those of other studies, including He and Kitchell (1990) and Chapleau et al. (1997).

We found that species vulnerable to predation in lakes without smallmouth bass were often more abundant relative

Fig. 2. Axes 1 and 2 from a correspondence analysis for summer survey lakes using XCPUE. Solid circles identify lakes containing smallmouth bass, and open circles identify lakes without smallmouth bass. See Table 2 for species abbreviations.



to populations in lakes with smallmouth bass, whereas most other species showed no clear trend in the abundance between these same lakes. Exclusion or reduction in abundance of species was limited to small-bodied species, whereas larger-bodied species (e.g., creek chub, yellow perch, and white sucker (*Catostomus commersoni*)) often coexisted with smallmouth bass populations. Blacknose shiner and bluntnose minnow, while often coexisting with smallmouth bass, were more abundant in lakes without smallmouth bass. Thus, predation by smallmouth bass has a greater influence on small-bodied species than on large-bodied species. This is consistent with He and Wright (1992), who observed a shift in community composition from small-bodied, soft-rayed species to large or deep-bodied species with spines following the introduction of northern pike.

Species subject to predation often seek refuge in structurally complex habitats (Crowder and Cooper 1982; McNair 1986). Although no statistically significant difference was found in habitat use of small-bodied species in lakes with smallmouth bass, a trend of greater abundance in complex habitat was observed. The fact that four of the six species considered vulnerable to smallmouth bass predation did not coexist with smallmouth bass limited the statistical power of this comparison. The complete absence of these species suggests that the lake conditions and habitat are insufficient to allow coexistence with smallmouth bass. In swimming all lakes, it was apparent that blacknose shiner and bluntnose minnow use the complex habitat to a greater degree than the simple habitat during the day. It is possible that these species take advantage of diel peaks in piscivore activity and feed in simple habitats during low light levels while the predators are less active (Naud and Magnan 1988). This would explain why traps were able to catch these small-bodied species when set overnight. However, these same species, when not subject to predation, do not confine themselves to complex habitats but occupy the entire littoral zone. Moreover, these same fish are often more abundant in simple rather than complex habitats. These results are consistent with other studies suggesting that high densities of vegetation and coarse and large woody structures offer refuge for small fish from predation (Crowder and Cooper 1982; Eklöv 1997). Fish will capitalize on resources throughout the lake where feasible, as restricting their foraging to only complex habitats would increase intra- and interspecific competition. This factor explains why we see vulnerable species more evenly dispersed between habitat types in lakes not influenced by smallmouth bass predation. Fish restricted to complex habitat may be unable to move between complex habitat patches to decrease intra- and inter-specific competition (Persson and Greenberg 1990). This implies that fish should use a greater range of habitats within the lakes; however, in lakes containing smallmouth bass, we see that the small-bodied species are reduced in their abundance, confined largely to the complex habitats, or simply not present.

From these results, we conclude that fish are choosing complex habitat to avoid predation because fish in lakes without smallmouth bass use both complex and simple habitat types. Presumably, those fish in simple habitats in lakes without smallmouth bass are taking advantage of additional food resources. In our small lakes, there is a negative relationship between the size of fish and structural complexity when fish are faced with predation. This indicates that smaller fish that are restricted to highly complex habitats would experience increased competition and less profitable foraging, whereas larger individuals of the same species are less prone to predation and can capitalize on other available resources in less complex habitats.

Our results highlight the importance of structural complexity as a habitat requirement of many littoral fishes, especially in the presence of littoral predators. Therefore, littoral habitat is particularly critical in lakes susceptible to fish introductions. Most species introductions occur in lakes with the most human activity (those containing cottages). These are the same lakes where cottage owners often remove both macrophytes and woody materials for a desired beach-like shoreline. Christensen et al. (1996) found that developed lakes with shoreline residences have lower densities of coarse woody debris compared with undeveloped lakes. Removal of such physical structures is known to have negative impacts on species composition and abundance of fish, benthos, and plankton communities in both freshwater and marine habitats (e.g., Poe et al. 1986; Everett and Ruiz 1993). Therefore, it is important to recognize the potential risk of local extinction and reduced species richness in developed lakes due to the combined stresses of predation pressure and lack of structured habitat.

Because the predation effect of smallmouth bass is so strong, presence–absence data provide valuable information pertaining to species–lake associations and are appropriate for most study objectives. However, relative abundance and length estimates may provide additional information on changes in species–lake relationships. Results of our study suggest that the introduction of smallmouth bass and other littoral piscivores to small lakes will lead to the marked reduction or elimination of those species most vulnerable to predation. Therefore, priorities should be identified for small lakes composed mainly of native, small-bodied species or diverse cyprinid communities and efforts be made to prevent the introduction of piscivores into these lakes and the alteration or homogenization of both lake habitat and fish communities.

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References

Allendorf, F.W. 1991. Ecological and genetic effects of fish introductions: synthesis and recommendations. Can. J. Fish. Aquat. Sci. **48**(Suppl. 1): 178–181.

Bryan, M.D., and Scarnecchia, D.L. 1992. Species richness, composition and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. Environ. Biol. Fishes, **35**: 329–341.

Chapleau, F., Findlay, C.S., and Szenasy, E. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. Ecoscience, **4**: 259–268.

Christensen, D.L., Herwig, B.R., Schindler, D.E., and Carpenter, S.R. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. Ecol. Appl. **6**: 1143–1149.

Christie, W.J. 1957. The bass fishery of Lake Opeongo. M.Sc. thesis, University of Toronto, Toronto, Ont.

Crossman, E.J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. Can. J. Fish. Aquat. Sci. **48**(Suppl. 1.): 46–57.

Crowder, L.B., and Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology, **63**: 1802–1813.

Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. **54**: 1520–1531.

Everett, R.A., and Ruiz, G.M. 1993. Coarse woody debris as refuge from predation in aquatic communities: an experimental test. Oecologia, **93**: 475–486.

Harvey, H.H. 1981. Fish communities of the lakes of the Bruce Peninsula. Int. Ver. Theor. Angew. Limnol. **21**: 1222–1230.

He, X., and Kitchell, J.F. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. Trans. Am. Fish. Soc. **119**: 825–835.

He, X., and Wright, R.A. 1992. An experimental study of piscivore–planktivore interactions: population and community responses to predation. Can. J. Fish. Aquat. Sci. **49**: 1176–1183.

Jackson, D.A. 1988. Fish communities of the Black and Hollow River watersheds, Ontario. M.Sc. thesis, University of Toronto, Toronto, Ont.

Jackson, D.A., and Harvey, H.H. 1989. Biogeographic associations in fish assemblages: local versus regional processes. Ecology, **70**: 1472–1484.

Jackson, D.A., Somers, K.M., and Harvey, H.H. 1992. Null models and fish communities: evidence of non-random patterns. Am. Nat. **139**: 930–951.

Jackson, D.A., Peres-Neto, P.R., and Olden, J.D. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. Can. J. Fish. Aquat. Sci. **58**: 157–170.

MacRae, P.S.D. 1999. A comparative approach to quantify the influence of smallmouth bass predation and habitat complexity on the structure of littoral fish assemblages. M.Sc. thesis, University of Toronto, Toronto, Ont.

McInerny, M.C., and Degan, D.J. 1993. Electrofishing catch rates as an index of largemouth bass population density in two large reservoirs. N. Am. J. Fish. Manage. **13**: 223–228.

McNair, J.N. 1986. The effects of refuges on predator–prey interactions: a reconsideration. Theor. Popul. Biol. **29**: 38–63.

Mittlebach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology, **62**: 1370–1386.

Naud, M., and Magnan, P. 1988. Diel-offshore migrations in northern redbelly dace, *Phoxinus eos* (Cope), in relation to prey distribution in a small oligotrophic lake. Can. J. Zool. **66**: 1249–1253.

Persson, L., and Greenberg, L.A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilus*) – roach (*Rutilus rutilus*) interaction. Ecology, **71**: 44–56.

Phelan, J.P., and Baker, R.H. 1992. Optimal foraging in *Peromyscus polionotus*: the influence of item-size and predation risk. Behaviour, **121**: 95–109.

Poe, T.P., Hatcher, C.O., Brown, C.L., and Schlosser, S.W. 1986. Comparison of species composition and richness of fish assemblages in altered and unaltered littoral habitats. J. Freshwater Ecol. **3**: 525–536.

Post, J.R., and Evans, D.O. 1989. Experimental evidence of size-dependent mortality in juvenile yellow perch. Can. J. Zool. **67**: 521–523.

Power, M.E., Matthews, J.M., and Stewart, A.J. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. Ecology, **66**: 1448–1456.

Ridgway, M.S., Shuter, B.J., and Post, E.E. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). J. Anim. Ecol. **60**: 665–681.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. The principles and practice of statistics in biological research. 3rd ed. W.H. Freeman and Company, New York.

Tonn, W.M., and Magnuson, J.J. 1982. Patterns in species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology, **63**: 1149–1166.

Tonn, W.M., and Paskowski, C.A. 1986. Size-limited predation, winterkill and the organization of *Umbra–Perca* fish assemblages. Can. J. Fish. Aquat. Sci. **43**: 194–202.

Tonn, W.M., Paskowski, C.A., and Holpainen, I. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. Ecology, **73**: 951–958.

Werner, E.E., Mittelbach, G.G., and Hall, D.J. 1981. The role of foraging profitability and experience in habitat use by bluegill sunfish. Ecology, **62**: 116–125.

Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, **64**: 1540–1548.

Whittier, T., and Hughes, R.M. 1998. Evaluation of fish species tolerances to environmental stressors in lakes in the northern United States. N. Am. J. Fish. Manage. **18**: 236–252.

Zaret, T.M., and Paine, R.T. 1973. Species introductions in a tropical lake: a newly introduced piscivore can produce population changes in a wide range of trophic levels. Science (Washington, D.C.), **182**: 449–455.