

Nearshore fish assemblages associated with introduced predatory fishes in lakes

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ABSTRACT

1. Changes to native fish assemblages in lakes are commonly associated with introduced predatory fishes. How fish assemblages change as multiple predatory species are introduced is not well understood.

2. This study investigated the relationship between the presence of introduced large-bodied predatory fishes (largemouth bass *Micropterus salmoides*, pike *Esox lucius*, rock bass *Ambloplites rupestris*, smallmouth bass *Micropterus dolomieu*, walleye *Sander vitreus*) and the composition of native fish assemblages in littoral areas of 40 lakes in Algonquin Provincial Park, Ontario, Canada. Fish assemblages were compared across lakes of different predator composition, and within lakes before and after recent predator invasions.

3. The presence of an introduced predator was associated with significantly different native fish assemblages across lakes, after controlling for environmental and spatial variables.

4. Native fish assemblages did not significantly vary across lakes with more than one predator species. Furthermore, while declines in native species richness over time were observed in a number of lakes, these were not associated with introductions of additional predators.

5. Several small-bodied species (brook stickleback *Culea inconstans*, fathead minnow *Pimephales promelas*, finescale dace *Chrosomus neogaeus*, and northern redbelly dace *Chrosomus eos*) consistently showed strong negative correlations with predator presence.

6. The results suggest that predatory fish introductions alter native fish assemblages and that this impact is consistent regardless of the number of predatory species introduced.

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INTRODUCTION

Human disturbances of lake ecosystems and fish communities are widespread (Schindler, 2001). Among the most prevalent human disturbance threatening aquatic biodiversity is the introduction of non-native species (Dextrase and Mandrak, 2006). In particular, introductions of large predatory fishes for commercial and recreational reasons are common, continuing, and global in occurrence (Lever, 1996; Eby *et al.*, 2006; Vitule *et al.*, 2009).

Numerous empirical studies show that dramatic changes in aquatic communities can result from novel predatory fish introductions. Diverse examples come from both tropical

(Zaret and Paine, 1973; Ogutuohwayo, 1990; Latini and Petreere, 2004) and temperate regions (Garcia-Berthou and Moreno-Amich, 2000; Takamura, 2007; Sanderson *et al.*, 2009). Correlational evidence suggests that large piscivores introduced outside their native ranges (e.g. largemouth bass *Micropterus salmoides*, pike *Esox lucius*, rock bass *Ambloplites rupestris*, smallmouth bass *Micropterus dolomieu*, and walleye *Sander vitreus*) structure fish assemblages in North American lakes by reducing the abundance and diversity of small-bodied littoral fish populations (Chapleau *et al.*, 1997; Whittier *et al.*, 1997; Findlay *et al.*, 2000; MacRae and Jackson, 2001; Jackson, 2002). Experimental evidence indicates that pike introductions, for example, can greatly reduce prey fish

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abundances through piscivory and forced emigration (He and Kitchell, 1990).

In many regions of the world, multiple fish introductions have increased non-native predator species richness (Eby *et al.*, 2006), with potential consequences for prey populations, community structure, and ecosystem functioning (Bruno and Cardinale, 2008). Resource partitioning, selection effects, and facilitation among predators can lead to reductions in prey populations as predator richness increases, while interference competition or intraguild predation can increase prey populations as the number of predator species increases (Eklov and VanKooten, 2001; Vance-Chalcraft *et al.*, 2007; Bruno and Cardinale, 2008). The effects of increases in predator richness on prey populations depend on predator identity and habitat (Schmitz, 2007). Evidence to date suggests that fish assemblages vary as the number of introduced predatory species increases: Whittier *et al.* (1997) and Findlay *et al.* (2000) showed declines in cyprinid species richness in lakes with one or two introduced predatory fish species (but not in lakes with three or more predators) compared with lakes with fewer predatory species. Given the context-dependence of predator richness effects on prey (Schmitz, 2007), the uncertainty in predicting outcomes of fish species interactions (Leprieur *et al.*, 2009) and continuing increases in non-native predator richness (Eby *et al.*, 2006), more work is needed to understand better the impacts of multiple predatory fish species introductions on recipient assemblages.

This study examined the effect of littoral predatory fish introductions on nearshore native fish assemblages in Algonquin Provincial Park, Ontario, Canada. As a result of the postglacial history of the region, a number of lakes in Algonquin Park lack native littoral, large-bodied piscivores (Mandrak and Crossman, 2003). Introductions of smallmouth bass to the lakes began in the early 1900s (Mandrak and Crossman, 2003). Since the 1980s, largemouth bass, pike, rock bass, and walleye have invaded lakes in the region through illegal stocking, possible bait-bucket introductions, and subsequent secondary dispersal (Mandrak and Crossman, 2003). In particular, this study assessed (1) differences in nearshore native fish assemblages across lakes in relation to introduced predatory fish presence, and (2) differences in nearshore native fish assemblages as introduced predator species richness increases across lakes and within lakes over time. It was hypothesized that lakes with introduced predators present would have significantly different native fish assemblages from lakes without introduced predators and that native fish assemblages would be further altered with additional predator introductions.

METHODS

Sampling methods

Nearshore fish assemblages were sampled in 40 lakes in Algonquin Provincial Park, Ontario, Canada, between 24 June and 23 August 2009. Of these, 37 were located in the Madawaska River catchment and the others (Heron, Scott, and Tea lakes) were in the Oxtongue River catchment (Table 1, Figure 1). Lakes were chosen based on the occurrence of invasive fish species, variation in environmental characteristics, and accessibility. Each lake was sampled once and four sites were sampled at each lake. Sites were chosen to reflect the

range of habitats (e.g. bog, beach) observed in a lake and, if few habitats were available, the most predominant habitat was sampled with multiple sites. Sampling at each site was conducted using daytime seine hauls (9.1 m bag seine with 6.3 mm mesh; five hauls per site and additional hauls until no new species were captured on the final haul), daytime short-set gillnets (9.1 m × 0.9 m gillnet with equal size panels of 13, 19, 25, 32, 38, 44, and 51 mm stretched mesh set for 0.5–1 h) and Gee minnow traps (four traps per site baited and set overnight). The chosen gillnet size is commonly employed in small fish monitoring programmes in Ontario (Metcalf, 2009); sets were of short duration to minimize fish mortality. Gee minnow traps are constructed of 0.5 cm metal mesh and are cylindrical (42 cm length by 22.5 cm width) with inverted cones at both ends with 2–3 cm openings. Each individual fish specimen captured was identified in the field and released when sampling at that site was completed or preserved in 70% ethanol and later identified following Scott and Crossman (1973). At least one specimen of each cyprinid species captured in a lake was preserved to ensure proper identification.

Data analysis – sampling sufficiency

Non-parametric estimators of species richness (first- and second-order Chao and Jackknife estimators) were used to estimate the proportion of the fish assemblage sampled (Colwell and Coddington, 1994). Studies have shown these four estimators to be generally unbiased, accurate, precise, and to perform better than other estimators (Walther and Moore, 2005). Total species richness for each lake was estimated using the sampling results of all gear types with 2000 permutations in *EstimateS* version 8.2 (Colwell, 2009) and the proportion of the estimated total number of species captured was calculated.

Data analysis – comparison across lakes

Data on 24 environmental variables were compiled for each lake (Table 2); these consisted of physical, chemical, habitat, and anthropogenic variables known to be correlated with fish assemblage structure (Jackson and Harvey, 1989; Pratt and Smokorowski, 2003; Taillon and Fox, 2004). Data for continuous variables were obtained from the Ontario Ministry of Natural Resources' Aquatic Habitat Inventory, which contains physical and chemical data for approximately 10 000 lakes in Ontario (Goodchild and Gale, 1981). The lakes in Algonquin Park were surveyed once or twice between 1968 and 1979 for the inventory. Average values for variables were used for lakes sampled twice. Square-root and \log_{10} transformations were applied to continuous variables as needed to ensure normal distributions (transformations listed in Table 2). Given that highly correlated independent variables in regression analyses can lead to spurious conclusions about their relationships with the dependent variable (Zar, 1999; Anderson *et al.*, 2008), variables highly correlated ($|r| > 0.7$) to at least one other independent variable were dropped from subsequent analyses (Zar, 1999). Of each pair of highly correlated variables, the variable with higher correlations with the remaining independent variables was excluded (maximum depth, perimeter, and total dissolved solids). Vegetation, substrate, woody debris, inflow, and cottage presence were assessed visually while sampling at each site and summarized as binary variables (listed in Table 2). Two binary variables, 'substrate-silt' and 'emergent vegetation – scattered', had the

Table 1. Changes in introduced predator species presence and native species richness from 1989–1991 to 2009

No. ^a	Lake name ^b	Old invaders ^c	New invaders
1	Annie Bay	smallmouth bass	
2	Billy		
3	Bluff		
4	Booth*	smallmouth bass	pike, rock bass
5	Brewer		
6	Bridle ^{ns}	smallmouth bass	pike, rock bass
7	Cache	smallmouth bass	
8	Canisbay ^{ns}	smallmouth bass	
9	Cauliflower ^{ns}		
10	Clarke	largemouth bass?, rock bass?	
11	Coon	rock bass?, smallmouth bass	
12	Costello ^{ns}		
13	Crotch ^{ns}	pike, smallmouth bass	largemouth bass, rock bass
14	Farm ^{ns}	pike, smallmouth bass	largemouth bass, rock bass
15	Galeairy	rock bass, smallmouth bass, walleye	largemouth bass, pike
16	Gordon	smallmouth bass	
17	Heron ^{ns}	smallmouth bass	
18	Kearney	smallmouth bass, rock bass?	
19	Kitty*	pike?, smallmouth bass	rock bass
20	Marmot		
21	Mew ^{ns}	smallmouth bass	
22	Oram		
23	Pen*		
24	Pog*	rock bass, smallmouth bass	
25	Provoking	smallmouth bass	
26	Rock*	rock bass, smallmouth bass	largemouth bass, walleye
27	Scott ^{ns}		
28	Shall	pike, smallmouth bass	largemouth bass, rock bass
29	Shirley*		
30	Source ^{ns}		
31	Speckled Trout	smallmouth bass	
32	Sproule		
33	Sunday ^{ns}		
34	Tanamakoon	smallmouth bass	
35	Tea*	smallmouth bass	
36	Tip Up	smallmouth bass	pike, rock bass
37	Two Rivers	rock bass, smallmouth bass	
38	West Smith ^{ns}		
39	Whitefish	rock bass, smallmouth bass	largemouth bass
40	Wright	smallmouth bass	

^aLake number refers to lake labels on Figure 1.

^bNative species richness in lakes with superscripts was compared in the ROM survey (1989–1991) with the 2009 survey. Asterisks indicate a significant decline in native species richness in 2009 relative to the ROM survey ($P < 0.05$ based on rarefaction curves). 'ns' indicates no significant change between surveys.

^c'Old invaders' refers to invaders established before the ROM 1989–1991 survey. 'New invaders' refers to an invader detected since the ROM survey. Question marks indicate instances of uncertain introduction times.

same value for every lake and were discarded. Marmot Lake was excluded from subsequent analyses using environmental variables owing to missing data. To control for potential spatial autocorrelation in fish communities (Legendre and Legendre, 1998), spatial variables were included in the analysis. A third-degree polynomial trend surface analysis of the geographic coordinates of the lakes was used to derive nine spatial variables (Legendre and Legendre, 1998).

Largemouth bass, pike, rock bass, smallmouth bass, and walleye presence was determined based on recent observations by Fisheries and Oceans Canada (unpublished data), Ontario Ministry of Natural Resources (unpublished data), Royal Ontario Museum (located in Toronto, Ontario, Canada), Mandrak and Crossman (2003), and the sampling results from this study (Table 1). Three predator variables were derived based on the introduced predator distributions. The first variable, PredPres, is a binary variable with the value of one if any introduced predator is present in a lake. The second

variable, PredRich, is the number of introduced predator species in a lake. The third variable, PredSMB, categorizes lakes as containing (i) no introduced predators, (ii) smallmouth bass only, or (iii) smallmouth bass with other introduced predators. PredSMB was used because every lake with predators contained smallmouth bass, with the exception of Clarke Lake (Table 1).

Catch data for native fishes were summarized for each lake as the presence–absence of each species. Presence–absence data are considered to be a more reliable measure of a fish assemblage than abundance data (Jackson and Harvey, 1997) and, thus, results from the presence–absence data are likely to lead to more robust findings than abundance data.

Distance-based linear modelling (DISTLM) in PERMANOVA+ for PRIMER 6.1 using distance-based redundancy analysis (dbRDA) was carried out to assess the relative contributions of environmental variables, spatial variables, and introduced predators in structuring fish assemblages across lakes (Legendre

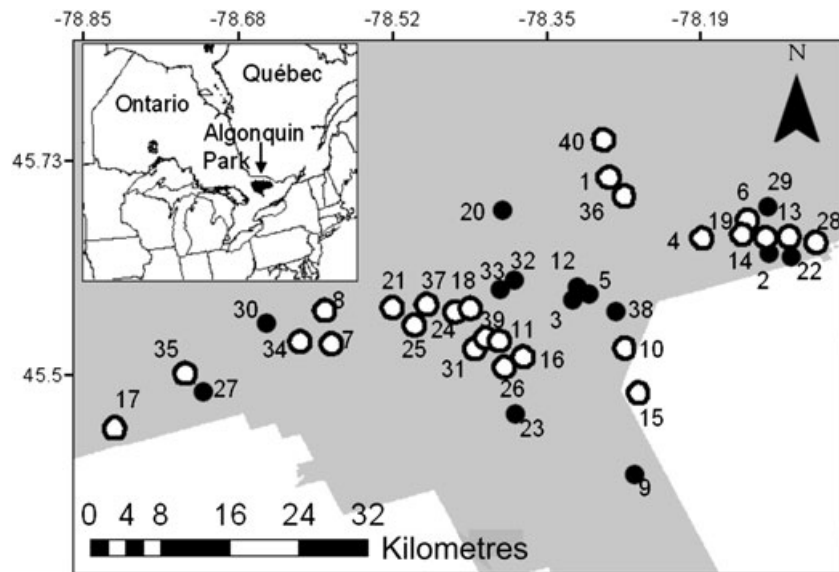


Figure 1. Location of sampled lakes with introduced predators (hollow circles) and without introduced predators (solid circles). The inset shows the location of Algonquin Provincial Park, Ontario, Canada which is coloured grey on the large map. Numbers refer to lake names listed in Table 1.

Table 2. Summary of lake variables

Variable ^a	Type	Range	Transformation	Retained as covariate? ^b
pH	Continuous	6.0–8.3		
Secchi (m)	Continuous	2.2–7.5		Yes
Conductivity ($\mu\text{S cm}^{-1}$)	Continuous	26–105	Log_{10}	
Total dissolved solids (mg L^{-1})*	Continuous	20.6–86.2	Log_{10}	
Surface area (km^2)	Continuous	0.04–8.9	Log_{10}	
Perimeter (km)*	Continuous	1.0–62.8	Log_{10}	
Maximum depth (m)*	Continuous	2.4–44.2	Square root	
Mean depth (m)	Continuous	0.9–16.8	Square root	
Elevation (m)	Continuous	366–473	Log_{10}	Yes
Shoreline development factor	Continuous	0.12–0.59	Log_{10}	
Emergent vegetation – none	Binary			
Emergent vegetation – scattered*	Binary			
Emergent vegetation – dense	Binary			Yes
Submerged vegetation – none	Binary			
Submerged vegetation – scattered	Binary			
Submerged vegetation – dense	Binary			
Substrate – silt*	Binary			
Substrate – sand	Binary			
Substrate – rock	Binary			Yes
Wood – none	Binary			
Wood – scattered	Binary			
Wood – dense	Binary			
Inflow – present	Binary			Yes
Cottages – present	Binary			

^aContinuous variables are from the Ontario Aquatic Habitat Inventory. Binary variables were assessed at each site sampled and then pooled for each lake. Variables marked with an asterisk were omitted from best subsets model selection routine due to collinearity or no variation.

^bEnvironmental variables were retained based on AIC best subsets routine. Spatial variables retained from AIC best subsets routine were X^2 and X^3 .

and Anderson, 1999; McArdle and Anderson, 2001). DISTLM allows for significance testing of explanatory variables for a multivariate response variable in the form of a resemblance matrix (Anderson *et al.*, 2008). In addition, DISTLM performs variation partitioning for sets of explanatory variables as in other canonical approaches such as redundancy analysis or canonical correspondence analysis (Anderson *et al.*, 2008). The native fish matrix based on presence-absence data was constructed using chi-square distance. Chi-square distance was chosen over other resemblance measures (such as Jaccard or

Sorenson) to avoid arch effects that were apparent in exploratory data analysis using principal coordinates analysis (Podani and Miklos, 2002). Rare species ($n = 2$, those found in $<5\%$ of lakes) were excluded from the analysis as they do not contribute to general patterns across lakes (Jackson, 2002). The best subsets model selection routine, with AIC as the selection criterion based on 9999 permutations in PERMANOVA+, was used to choose a reduced number of environmental and spatial variables for subsequent analysis (chosen variables listed in Table 2). The amount of variation across fish assemblages

explained by the chosen spatial and environmental variables and each predator variable was tested by fitting the variables sequentially with DISTLM; significance testing was based on 9999 permutations. Permutational multivariate analysis of variance (PERMANOVA) was used to test the significance of the PredSMB term, and sequential Bonferroni corrected (Holm, 1979) pairwise comparisons of group means were completed in the case of a significant result to assess which levels of the factor were significantly different. Plots of the first two dbRDA axes were examined to determine how introduced predator presence and specific native species were related.

Data analysis – comparison across time

Extensive fish community surveying was completed in Algonquin Provincial Park in 1989–1991 by the Royal Ontario Museum (ROM). Of the 40 lakes sampled in 2009, 21 had been sampled in the ROM survey. Predatory fishes have invaded a number of these lakes since 1989. Although a wider variety of habitats was sampled and more gear types were used in the ROM surveys than in 2009, only seine haul data from both surveys were considered for purposes of comparison. This restriction ensured that only data from shallow (1 to 2 m), nearshore habitats would be compared and that gear biases would not affect comparisons across surveys. The proportion of species detected in each lake with seine hauls was calculated using first- and second-order Chao and Jackknife species richness estimators. The timing of predator introductions was estimated using recent Fisheries and Oceans Canada and Ontario Ministry of Natural Resources sampling (unpublished data), Mandrak and Crossman (2003), ROM survey results, and the results from the 2009 survey.

Individual-based rarefaction curves were calculated using 2000 iterations from each lake's ROM and 2009 survey results in *Ecosim* 7.0 (Gotelli and Entsminger, 2009). Individual-based rarefaction curves scale species richness to the number of individuals captured and, thus, are appropriate to use when sampling effort is different across surveys (Gotelli and Colwell, 2001). 95% confidence intervals were used to determine whether native species richness was significantly different in the two surveys for the same number of sampled individuals (Gotelli and Entsminger, 2009). The proportions of lakes showing significant decreases in species richness with and without 'new' invasions (i.e. since the ROM survey) were compared with a one-tailed Fisher Exact Test, with the a priori alternative hypothesis that more lakes with new invasions would show decreases in native species richness.

RESULTS

Sampling sufficiency

In total, 24 069 individual fishes representing 23 species (including non-native fishes) were captured in 2009 (Table 3); 2 to 14 species were captured per lake. Of the four sample-based non-parametric estimators of species richness used, Chao 1 and Jackknife 2 on average gave the lowest and highest estimates of total native species richness, respectively. The average proportion of native species captured with all gear types combined compared with the estimated species richness was 97% for Chao 1 and 80% for Jackknife 2.

Table 3. List of species captured in 2009 sampling

Scientific name	Common name	Abbreviation
<i>Chrosomus eos</i>	northern redbelly dace	RD
<i>Chrosomus neogaeus</i>	finescale dace	FD
<i>Luxilus cornutus</i>	common shiner	CS
<i>Margariscus nachtriebi</i>	northern pearl dace	PD
<i>Notemigonus crysoleucas</i>	golden shiner	GS
<i>Notropis heterodon</i>	blackchin shiner	BC
<i>Notropis heterolepis</i>	blacknose shiner	BN
<i>Pimephales notatus</i>	bluntnose minnow	BM
<i>Pimephales promelas</i>	fathead minnow	FM
<i>Semotilus atromaculatus</i>	creek chub	CC
<i>Semotilus corporalis</i>	fallfish	FF
<i>Catostomus commersonii</i>	white sucker	WS
<i>Ameiurus nebulosus</i>	brown bullhead	BB
<i>Esox lucius</i>	pike	
<i>Umbra limi</i>	central mudminnow	CM
<i>Salvelinus fontinalis</i> ^a	brook trout	BT
<i>Culaea inconstans</i>	brook stickleback	BS
<i>Ambloplites rupestris</i>	rock bass	
<i>Lepomis gibbosus</i>	pumpkinseed	PS
<i>Micropterus dolomieu</i>	smallmouth bass	
<i>Micropterus salmoides</i>	largemouth bass	
<i>Etheostoma exile</i> ^a	Iowa darter	ID
<i>Perca flavescens</i>	yellow perch	YP

^aSpecies captured in less than 5% of lakes.

Fish assemblage comparison across lakes

Distance-based linear modelling variation partitioning showed that environmental and spatial variables explained more variation than predator variables (full results are provided in Figure 2). However, predator presence (PredPres) was a significant predictor of fish assemblage differences, explaining 5.9% of the variation in native fish species presence–absence data ($F_{\text{pseudo}} = 2.9$, $df = 30$, $P = 0.0028$, $n = 39$) after adding environmental and spatial variables. PredPres was most strongly correlated with the first dbRDA axis and was more strongly correlated with this axis than any other explanatory variable (multiple partial correlation = -0.86). Several species showed strong positive correlations (Spearman correlations) with this axis (i.e. in the opposite direction of PredPres):

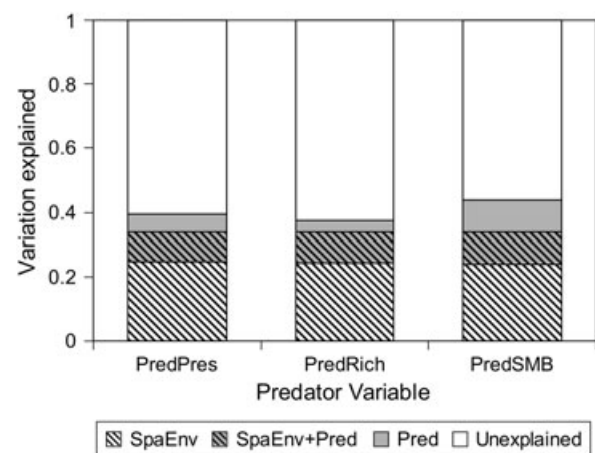


Figure 2. Variation partitioning from distance-based linear modelling for native fish presence–absence. SpaEnv, variation split between purely spatial and environmental variables. SpaEnv+Pred, variation shared between spatial and environmental and predator variables. Pred, variation of purely predator variables.

northern redbelly dace (0.74); finescale dace (0.52); fathead minnow (0.55); and brook stickleback (0.44) (Figure 3). After adding environmental and spatial variables, predator species richness (PredRich) was a marginally significant predictor of fish assemblage differences ($F_{\text{pseudo}}=1.7$, $df=30$, 3.6% of variation, $P=0.074$, $n=39$ lakes). With environmental and spatial covariates, the one-factor PERMANOVA (with (i) no predator, (ii) smallmouth bass only, (iii) smallmouth bass + other predators as levels) showed that fish assemblages varied significantly across the three levels of the factor (PredSMB), explaining 10.0% of variation ($F_{\text{pseudo}}=2.5$, $df=28$, $P=0.0013$, $n=38$ lakes). Pairwise comparisons showed no significant differences between predator groupings at the sequential Bonferroni adjusted $P=0.05$ significance level. However, it is clear that most of the differences across groupings were due to lakes with (i) no predators vs. (ii) smallmouth bass only ($P=0.061$) and (i) no predators vs. (iii) smallmouth bass + other predators ($P=0.057$) and not lakes with (ii) smallmouth bass only vs. (iii) smallmouth bass + other predators ($P=0.79$).

Fish assemblage comparison across time

Two of the 21 lakes sampled in the 2009 and ROM surveys, Cache Lake and Galeairy Lake, had very low total abundances of native fishes ($n < 7$) in one survey. These lakes were excluded from analysis because rarefaction curves always converge at low abundances, making comparisons at low abundances uninformative (Gotelli and Colwell, 2001). Of the lakes retained for analysis, six had new introduced predatory species detected between the ROM and 2009 surveys. All six lakes with new invasions had at least one introduced predator present before the ROM survey. Thirteen lakes had no new introduced species detected; five of these had 'old' invasions occurring before the ROM survey, and eight had no invasions (Table 1). In no case between 1989 and 2009 was a predator introduced into a lake previously free of introduced predators. Of the four species richness estimators used, the lowest average proportion of total species captured in the ROM survey was estimated to be 71%, using the Chao 2 estimator, and the highest was 92%, using the Chao 1 estimator.

Three lakes with new invasions showed a reduction in native species richness over time ($P < 0.05$). Reduced species richness over time was also observed in four lakes without new invasions, including two that had old invasions and two that had no recorded invasions (Table 1). No lakes showed a significant increase in species richness. The proportion of lakes showing significant declines in species richness was not different between those with a new invasion and those without a new invasion (one-tailed Fisher's exact test, $P=0.38$), nor was it significantly different in lakes with no invasions, old invasions only, and new invasions (χ^2 test, $\chi^2=0.96$, $P=0.62$).

DISCUSSION

Introduced predator presence explained a significant amount of variation in native nearshore fish assemblages, after controlling for environmental and spatial variables. Small-bodied fish species (brook stickleback, fathead minnow, finescale dace, and northern redbelly dace) showed the strongest negative correlations with predator presence. Native fish assemblages associated with multiple introduced predatory species were no different from those associated with a single introduced predator, and changes in fish assemblages over time were not associated with additional predator introductions.

Relative importance of predators, environment, and space

There was support for the hypothesis that native fish assemblages vary with the presence of introduced predatory fishes after controlling for environmental and spatial variables. A considerable amount (24 to 24.7%) of the variation across lakes was explained by environmental and spatial variables, which exceeded that explained purely by predator variables ($\leq 10\%$). The amount of variation shared by environmental, spatial, and predator variables was 9.0 to 9.8%. Introduced predators play a role in structuring fish assemblages; after controlling for environmental and spatial terms, the predator presence-absence variable (PredPres) was significant. Furthermore, while environmental and spatial variables altogether explained more variation than PredPres, PredPres was the

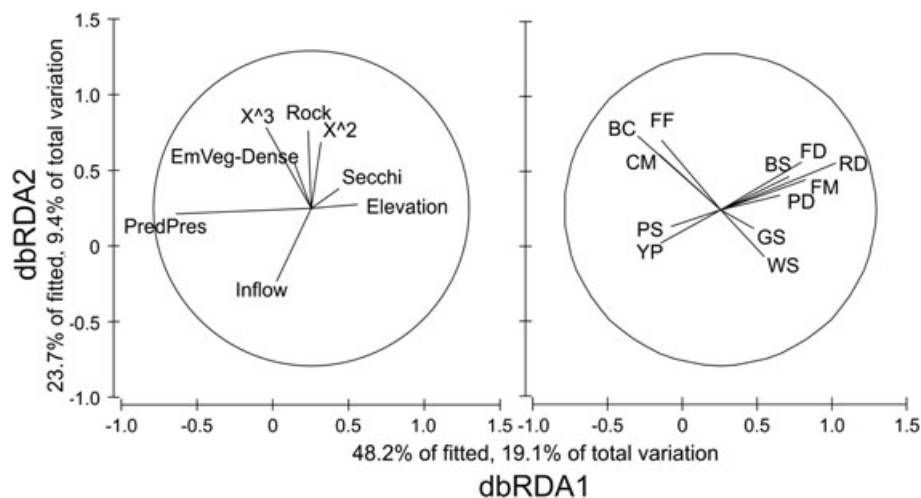


Figure 3. The first two axes of the distance-based redundancy analysis (dbRDA) of native fish presence-absence data with explanatory variable (left) and species (right) correlations. Only species with correlations >0.25 with either axis are plotted. Vector length represents correlation strength; the circle shows a correlation of 1. Species abbreviations refer to Table 3.

most important *single* explanatory variable and accounted for most of the variation along the first axis of the distance-based redundancy analysis.

Overall, environmental and spatial factors played a stronger role than introduced predators in determining fish assemblage structure in the sampled lakes. Conclusions about the relative roles of predation and abiotic variables can change at different scales of observation; biotic factors tend to be more important in structuring fish communities at smaller scales, while abiotic factors dominate at larger scales (Jackson and Harvey, 1989; Jackson *et al.*, 2001). Although the sampled lakes were on a relatively small spatial scale (the two furthest lakes were ~60 km apart), environmental and spatial variables could explain much of the variation in fish assemblages across lakes. Interestingly, a study from an Iberian catchment found similar results when comparing the importance of environmental variables to introduced fishes in structuring native fish communities: 24.4% of the variation in the Iberian fish communities was explained by environmental variables, 12.4% was explained by introduced fishes, and 9.2% of the variation was explained jointly by environment and introduced fishes (Godinho and Ferreira, 1998).

Predator richness effects

Comparisons across lakes and across time do not support the hypothesis that additions of predator species to already invaded lakes are associated with changes in native fish assemblages. Predator richness (PredRich) did not explain more variation across fish assemblages than did predator presence (PredPres) and the PERMANOVA results showed that most of the differences in fish assemblages were a result of differences in lakes with and without predators, not between lakes with varying numbers of predator species. The temporal comparison showed that declines in native species richness were unrelated to additional predator introductions.

There are several possible explanations for the lack of a predator richness effect. Native fish populations might have been affected by predator richness in ways too subtle to be detected in an analysis based on presence-absence data. For example, the addition of predators to lakes already containing introduced smallmouth bass may have caused minor declines in the abundance of several native species rather than affect the presence of those species. A second possibility is that the introduced predators in the study were functionally similar such that additional predator species would contribute no new impacts on the fish community. Third, the apparent lack of a predator richness effect could reflect a time lag in impact (Strayer *et al.*, 2006). All predators, apart from smallmouth bass, were introduced relatively recently – within the last few decades – and many probably only several years before the 2009 survey. Fish communities may not yet have fully adjusted in response to the new predator regimes, although He and Kitchell (1990) found that pike drove large changes in prey abundance within a year after introduction in a small lake. Fourth, because smallmouth bass is found in almost every lake with other predators, smallmouth bass alone could be driving the change in fish assemblages. However, the other predators in this study are highly piscivorous (Scott and Crossman, 1973) and have been shown to structure fish communities elsewhere (Robinson and Tonn, 1989; He and Kitchell, 1990). Finally, it is possible that interactions between predators, such as

intraguild predation or interference competition, could be reducing predators' foraging effectiveness (Bruno and Cardinale, 2008). This possibility cannot be assessed without more information on predators' diet and behaviour.

Species-specific responses to predator introduction

Several species (brook stickleback, fathead minnow, finescale dace, and northern redbelly dace) showed strong negative correlations with introduced predators, consistent with other studies (He and Kitchell, 1990; MacRae and Jackson, 2001; Jackson, 2002). Similarly, a laboratory study showed brook stickleback, fathead minnow, and finescale dace to be more vulnerable than yellow perch to pike predation, probably because of differences in morphology and behaviour (Robinson, 1989). In the 2009 survey, finescale dace and northern redbelly dace were never detected in a lake with an introduced predator, and fathead minnow and brook stickleback were found in only two and three of the 26 lakes with an introduced predator, respectively. It is unclear whether populations of these 'predator-vulnerable' species are completely extirpated by introduced predators or driven to abundances below the detection limits of the sampling effort. Alternatively, the pattern might be driven by a confounding factor affecting both predator and prey distributions (see *Drivers of fish assemblage patterns* below).

Trait differences can explain why certain species tend not to co-exist with predators. Increased susceptibility to predation is generally attributed to small body size (Tonn and Magnuson, 1982; He and Kitchell, 1990; Chapleau *et al.*, 1997). The average length of 'predator-vulnerable' species ranges from 50 mm (for brook stickleback and fathead minnow) to 75 mm (for finescale dace) (Holm *et al.*, 2009). In contrast, the presence of large-bodied cyprinids such as fallfish, creek chub, common shiner, and golden shiner (average length ranging from 90 mm for common shiner to 200 mm for fallfish) is not negatively correlated with predators. This suggests a size refugium from predation. The lack of spiny rays in cyprinids might also increase their vulnerability to predation (Tonn and Magnuson, 1982; He and Kitchell, 1990; Chapleau *et al.*, 1997). Anti-predator behaviours, such as evasive swimming and maintaining large distances from predators, have also been shown to reduce prey fishes' vulnerability to predation (Wahl and Stein, 1988). If this trait-based interpretation is correct, it suggests that not only does the species composition of predator-invaded communities change but also their ecological traits (Eros *et al.*, 2009).

Factors affecting apparent changes in species richness

It is unclear why some lakes, both with and without introduced predators, showed significant reductions in species richness over 20 years. Natural fluctuations in fish populations could be causing species' abundance to drop below detectable levels, thereby suggesting reduced species richness (Magnuson *et al.*, 1994), but the natural range of variability cannot be assessed with only two 'snapshot' measures of each lake's fish assemblage. The 2009 survey may have sampled lakes that were in a period of low fish abundance relative to the time of the ROM surveys. However, fluctuations should have also resulted in increased abundance (and thereby apparent increases in species richness) in some lakes between the two surveys. On the other hand, large-scale external drivers, such as

changes in climate and biogeochemical cycling, could be causing decreases in species abundance or richness over time; such stressors have been linked with changes in aquatic communities in the nearby Dorset region (Yan *et al.*, 2008). Large-scale stressors seem a possible explanation for the apparent changes in fish species richness, but the decline in species richness was observed in relatively few lakes. Alternatively, the observed pattern could be caused by small-scale, lake-specific stressors such as hypoxia, which can cause large declines in small fish abundances (Danylchuk and Tonn, 2003). Species detection differences between the surveys might also explain apparent declines in species richness; however, based on species richness estimators, a greater proportion of species present were captured on average in the 2009 survey than the ROM survey.

Undetected fish introductions could also drive changes in species richness in lakes without any recorded introduced predators. While introductions would initially increase species richness, interactions between invaders and native species could reduce species richness over time. A long-standing ban on live baitfish in Algonquin Park reduces the likelihood of introduced minnows being present in any of the lakes (Mandrak and Crossman, 2003). Several species that rarely occur in nearshore habitats in the summer – cisco *Coregonus artedii* and splake *Salvelinus fontinalis* × *S. namaycush* – have been introduced to some of the sampled lakes and some populations of brook trout *Salvelinus fontinalis* are maintained by stocking. While splake and brook trout can feed on minnows, Jackson (2002) found that their presence is not associated with significantly decreased cyprinid richness.

Drivers of fish assemblage patterns

A negative correlation between predator and prey species does not by itself indicate that predation reduces prey richness. If confounding variables are not controlled, observed patterns in fish assemblages can be a result of factors correlated with predator presence. For example, northern redbelly dace tend to prefer boggy habitats with silt bottoms, but such habitats probably lack suitable spawning substrate for smallmouth bass, which nests on sand, gravel or rock substrate (Scott and Crossman, 1973). This could explain the strong negative correlation between predators (like smallmouth bass) and northern redbelly dace across lakes. Nevertheless, predation is probably an important driver of fish assemblage structure. The amount of variation in fish assemblages explained by predator variables was assessed after the spatial and environmental variables were added, and thus was not confounded. Moreover, a number of studies have also found negative correlations between predatory fishes and small fish diversity, supporting the interpretation that predation is a driver of fish assemblage structure (Chapleau *et al.*, 1997; Whittier *et al.*, 1997; Findlay *et al.*, 2000; MacRae and Jackson, 2001; Jackson, 2002). For example, He and Kitchell (1990) showed that a large change in the fish community following an experimental pike introduction to a previously predator-free lake was attributable to both the direct and indirect effects of predation.

The abundance of an introduced predator might be an important predictor of changes to native fish assemblages, as the impact of an invasive species is often correlated with its population size (Parker *et al.*, 1999). Declines in predatory fish abundance can result in increased prey fish populations (Weidel

et al., 2007). This study considered only the presence–absence and species richness of introduced predators. Low predator abundance in some lakes could explain the occasional co-occurrence of ‘predator-vulnerable’ brook stickleback and fathead minnow with predators. Furthermore, if the overall predator abundance across species is constrained, then lakes with more predator species would not have more individual predatory fishes (of any species) compared with lakes with fewer predators. This could explain the similarity in native fish assemblages in lakes with different numbers of introduced predator species.

Historical factors, such as postglacial colonization, play an important role in fish community structure (Moyle and Cech, 2004). Although the effects of historical factors are most evident at large spatial scales (Jackson and Harvey, 1989), three of the lakes sampled in Algonquin Park were in a catchment separate from the remaining lakes. There could be differences in the fish assemblages in the lakes of the two catchments owing to variation in postglacial colonization. However, exploratory data analysis showed the three Oxtongue catchment lakes did not separate out from the other lakes in principal coordinates plots of fish assemblages. Furthermore, DISTLM results were consistent regardless of whether the entire lake dataset was used or if the Oxtongue lakes were excluded.

Lake connectivity can also be a driver of fish assemblage patterns. While lakes are often considered isolated units, fishes have been shown to move between connected water bodies (Daniels *et al.*, 2008). Spatial autocorrelation resulting from fish movement between lakes was controlled in the analysis by the inclusion of spatial terms. In addition, fish populations can show source–sink dynamics, which occurs when the extirpation of populations in marginal habitats is prevented by the immigration of individuals from more optimal habitats (Woodford and McIntosh, 2010). Source–sink dynamics can allow the coexistence of a vulnerable native prey species with introduced piscivores (Woodford and McIntosh, 2010). The occasional findings of ‘predator-vulnerable’ species in lakes with introduced predators in the study may be explained by prey populations, living in the small ponds and streams that are connected to some of these lakes, that can maintain downstream sink populations negatively affected by predation.

Management implications

Results of this study showed that lakes with introduced littoral predators contain different fish assemblages from lakes without introduced predators. Importantly, a number of small-bodied species, such as brook stickleback, fathead minnow, finescale dace, and northern redbelly dace, are probably extirpated or severely reduced in abundance by predation. Introductions of littoral predators into lakes containing these species should be avoided by managers seeking to conserve native fish species.

Multiple predatory fish species seem to have no additional effect on fish assemblages compared with single predators. Therefore, if conservation resources are limited, efforts to prevent predatory fish introductions should be focused on lakes with no littoral predatory fish species already present. However, largemouth bass, pike, rock bass, smallmouth bass, and walleye have differing preferences for other aquatic prey such as amphibians and macroinvertebrates (Hodgson *et al.*, 1997; Soupir *et al.*, 2000). It remains to be determined whether adding predators to lakes already containing introduced predators has effects on aquatic organisms other than littoral small fishes.

The ranges of littoral predatory fishes will probably continue to expand. Suitable thermal habitat for warmwater species like smallmouth bass will be found throughout North America by 2100, owing to climate change (Sharma and Jackson, 2008). To preserve vulnerable native fish assemblages, fisheries managers must reduce both authorized and unauthorized predator introductions.

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