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Spatio-temporal changes in littoral fish community structure along the St. Lawrence River (Québec, Canada) following round goby (*Neogobius melanostomus*) invasion

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This study was contributed in relation to the 20th International Conference on Aquatic Invasive Species held in Fort Lauderdale, Florida, USA, October 22–26, 2017 (http://www.icais.org/html/previous20.html). This conference has provided a venue for the exchange of information on various aspects of aquatic invasive species since its inception in 1990. The conference continues to provide an opportunity for dialog between academia, industry and environmental regulators.

Abstract

The round goby (*Neogobius melanostomus*), a small Ponto-Caspian bottom-dwelling fish species, was first observed in the St. Lawrence River in 1997. After twenty years, it is now considered as one of the most successful invaders of the St. Lawrence River. Despite the elevated abundances observed throughout the river, little is known about its impacts on the littoral/mid-shore fish community. In this study, we used a large dataset obtained from an annual standardized fish survey held in the St. Lawrence River to analyze the impacts of round goby on littoral native fish community and native predator assemblages within five distinct segments of the river characterized by different round goby abundances. Throughout the system, the round goby negatively impacted the abundances of tessellated darter (*Etheostoma olmstedi*) likely as a consequence of competitive exclusion. In contrast, the small pelagic/demersal brook silverside (*Labidesthes sicculus*) and emerald shiner (*Notropis atherinoides*) increased in abundance. Indirect food web effects, such as predation pressure relaxation, are suspected. Native predator abundances exhibited contrasting trends in the different sectors analyzed, with the exception of smallmouth bass (*Micropterus dolomieu*) abundances that increased in all fluvial lakes. We hypothesize that trophic relationships between littoral fish and native predators are influencing the outcomes of the round goby invasion of the St. Lawrence River.

Key words: biological invasion, biodiversity, native predator, competition, fish monitoring

Introduction

Since the first detection in 1990 in St. Clair River (Michigan), the round goby (*Neogobius melanostomus*), a small benthic Ponto-Caspian fish, has reached such abundance and range expansion to become a major component of the Great Lakes ecosystem (Barton et al. 2005; Charlebois et al. 2001; French and Jude 2001; Jude et al. 1992). This small fish (10–135 mm) was likely introduced through ballast waters of transoceanic vessels travelling from the Black Sea (Charlebois et al. 2001; Jude et al. 1992). The demographic explosion observed in the Great Lakes severely impacted the fish and macroinvertebrate communities (Barton et al. 2005; Burkett and Jude 2015). In 1997, the first round goby was captured in Québec. Surprisingly, it was caught at the downstream end of the freshwater portion of the St. Lawrence River near Québec City in a commercial fishing weir exploited by the *Aquarium du Québec*.

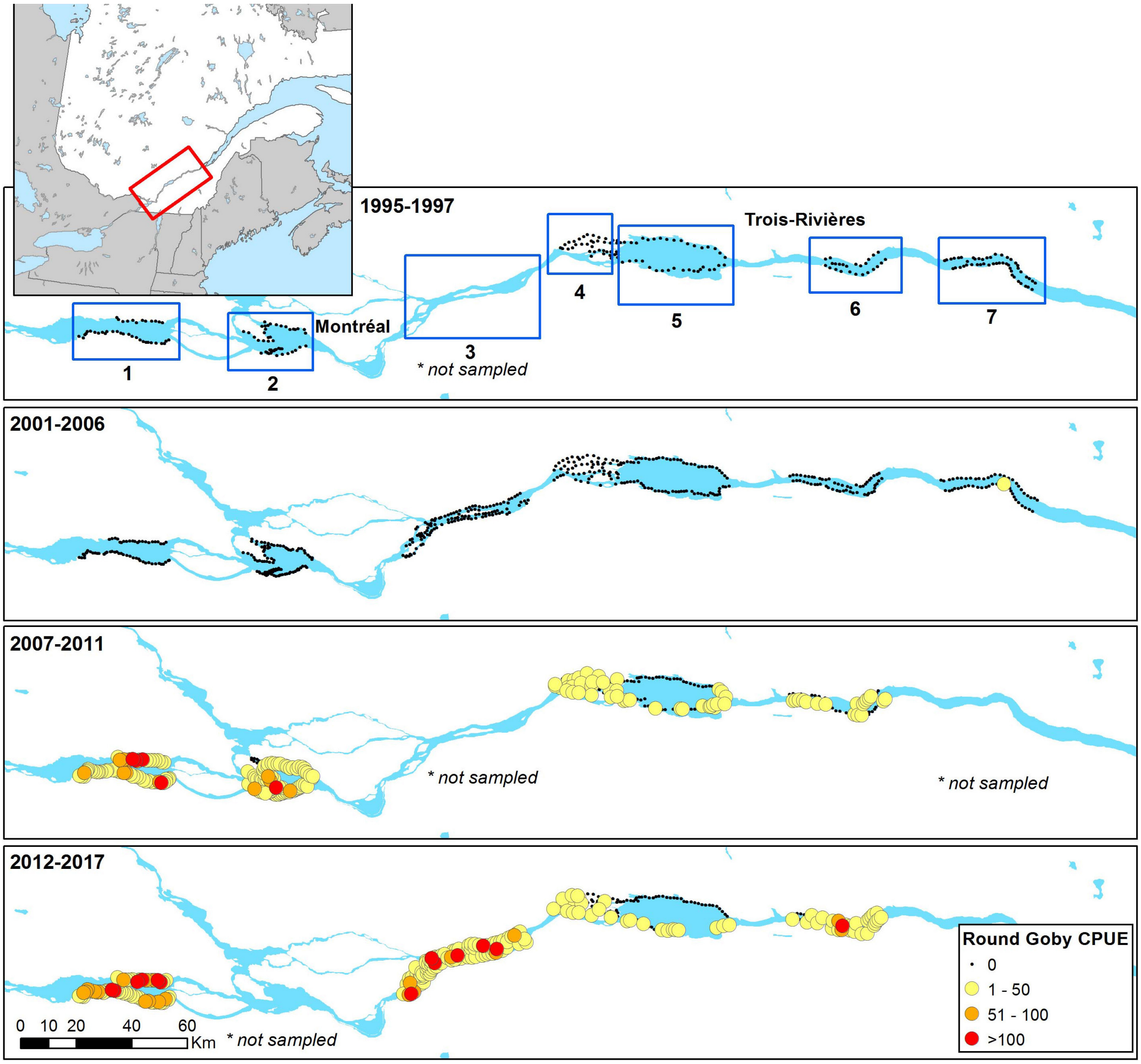

Figure 1. Maps of sampled fluvial sectors showing abundance of round goby for the four sampling cycles between 1995 and 2015. Sectors sampled are; (1) Saint-François Lake, (2) Saint-Louis Lake, (3) Montréal-Sorel, (4) Saint-Pierre Lake archipelago, (5) Saint-Pierre Lake, (6) Bécancour-Batiscan and (7) Grondines-Saint-Nicolas. Each circles/dots are showing sampled stations and round goby abundance; black dots are 0 capture, yellow is 0 to 50 captures, orange 50 to 100 captures and red over 100 captures.

It took a further three years before a second fish was reported; the fish was captured in the upstream fluvial Lake Saint-François in 2000. After that, gobies were observed in the St. Lawrence River surrounding Montréal in 2004. In 2006, nine years after the first capture in the St. Lawrence River, round goby were detected for the first time in the Grondines–Saint-Nicolas sector (Figure 1). From 2007 to 2011, the species rapidly colonized all freshwater sectors of the St. Lawrence River. Despite its prevalence in the St. Lawrence River, the impacts of round goby on littoral fish biodiversity and community structure have not yet been studied. It is hypothesized that differences observed in round goby abundance throughout the St. Lawrence River are related to the species' habitat preferences, diet plasticity and predation (Brodeur et al. 2011; Kipp et al. 2012; Reyjol et al. 2010).

The round goby is a territorial and aggressive benthic feeder believed to be a serious competitor of small benthic littoral fishes, particularly darters (*Etheostoma* spp.) and sculpins (*Cottus* spp.), since they exhibit similar diets and exploit the same habitats (Jude et al. 1992; Poos et al. 2010). Evidence for logperch (*Percina caprodes*) competitive exclusion on rocky substrate has been shown in Lake Superior (Leino and Mensinger 2016, 2017). In Lake St. Clair and Lake Michigan, round goby have notoriously extirpated mottled sculpin (*Cottus bairdii*) through competitive interactions, egg predation and territorial exclusion. However, the consequences of the round goby invasion throughout the Great Lakes region have been highly context-dependent. Hence, some tributaries of Lake Michigan showed no temporal trend in native benthic abundance despite the increase in round goby abundance (Kornis et al. 2013). After establishment, round goby could represent an important component of the littoral and benthic fish community, being equally represented in the diet of predatory fishes as native species (Johnson et al. 2005b; Lauer et al. 2004). In Lakes Erie and Ontario, smallmouth bass (*Micropterus dolomieu*) and burbot (*Lota lota*) diet is now based to a large extent on round goby, resulting in a general increase in body condition and mean total length at age (Crane and Einhouse 2016; Crane et al. 2015; Johnson et al. 2005b). However, the effects on predator community have been variable among species (Kornis et al. 2013). Some authors suggest that predation on round goby could have mitigated their deleterious effects (Brodeur et al. 2011; Madenjian et al. 2011; Reyjol et al. 2010), a hypothesis that remains to be tested.

The present study assessed the potential long-term impacts of round goby on littoral fish community structure within the heterogeneous riverscape of the St. Lawrence River. Changes in species assemblages in relation to variable round goby densities in five major sectors of the St. Lawrence River were quantified using multivariate analysis. We hypothesized that changes in littoral fish assemblage following the round goby invasion could be related to food web interactions involving the native predator community. We thus examined the effect of round goby presence on both the littoral fish assemblages and local native predators.

Methods

Fish abundances were obtained from the RSI, a governmental fish survey conducted in the St. Lawrence River ("Réseau de Suivi Ichtyologique", described in La Violette et al. 2003) that characterizes the fish community at the end of the growing season (August to October). Since 1995, this annual standardized survey has routinely been used for assessing stock status, fish biodiversity and the overall health of fish communities (index) along the St. Lawrence River (Foubert et al. 2018; La Violette et al. 2003). Given the sheer size of the system, the entire river was not sampled every year. Hence, the freshwater portion of the St. Lawrence River was divided into seven different sectors according to their specific hydrological and morphometric characteristics (Figure 1); one or two of these sectors were sampled in a given year. Between 1995 and 2015, the entire St. Lawrence River was sampled four times (four sampling cycles are now completed, the latest cycle started in 2016).

The RSI sampling strategy was designed to cover both lentic and lotic habitats in all sectors along both shores of the St. Lawrence River. The deep navigation channel was excluded (see de la Chenelière et al. 2014). The RSI used two different gears according to the position of the sampling station (1) a standardized beach seine net (12.5 m long × 4 m deep and 3.2 mm stretched mesh) and (2) an array of two multimesh gillnets (60 m long × 1.8 m deep; eight panels of 25, 38, 51, 64, 76, 102, 127 and 152 mm stretched mesh; La Violette et al. 2003). Samples were collected at approximately every km of shoreline. Seine nets were used for sampling the lentic community in nearshore littoral habitats (depth < 1.5 m), while gillnets were used for sampling lentic and lotic midshore littoral habitats in the deeper water column (between 1.5 and 14 m depth). Each seine net cast corresponds to a total sampled surface of approximately 120 m^2. Littoral fish and round goby abundance were calculated as catch per unit effort (CPUE), corresponding to number of fish per seine net haul. Native predators from midshore lotic habitats were more efficiently captured using experimental gillnets. Gillnets were deployed overnight, next to the beach seine stations for 15.0 to 28.5 hours (La Violette et al. 2003); an overnight fishing session at one site corresponds to one (1) unit of effort. Native predator CPUEs were calculated as fish number per night, per gillnet. For subsequent analyses, six species were considered as potential native predators for round goby based on the literature (Kornis et al. 2012; Reyjol et al. 2010); sauger (*Sander canadensis*), walleye (*Sander vitreus*), smallmouth bass, largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*). The dataset considered in the present study included 19 experimental units (year * sector) covering 22 years (from 1995 to 2017) totalling 1350 seine samples with an average of 71.05 seine net samples per experimental unit. A total of 272,971 individuals from 73 fish species were captured. The gillnet dataset included 2221 units of effort which resulted in the capture of 33,142 individuals belonging to the six predatory species listed above (Table 1).

We quantified the changes in the littoral fish community structure (using only seine samples) following round goby invasion by comparing the species assemblages before and after establishment within the five most-impacted fluvial sectors; Lake Saint-François,

Table 1. Sampling information (year, number of seine and gillnet stations) and diversity metrics by sector sampled and information on round goby abundance (CPUE), calculated metrics are species richness, Shannon index (H), Simpsons index (1-D), and Pielou's evenness (J).

Sector	Year	Seine (n)	Gillnets (n)	Round goby (CPUE)	Richness	H	1-D	J
Bécancour-Batiscan	1996	26	43	0.00	28	3.31	0.85	0.69
	2001	59	65	0.00	34	2.41	0.66	0.47
	2008	57	130	**3.09**	44	3.89	0.91	0.71
	2012	57	129	**9.25**	39	2.94	0.79	0.56
	2017	57	127	**4.75**	42	2.75	0.69	0.51
Saint-Pierre Lake	1995	36	57	0.00	26	3.29	0.87	0.70
	2002	72	131	0.00	40	3.19	0.83	0.60
	2007	73	231	**1.45**	42	3.34	0.87	0.62
	2013	72	232	**0.76**	44	3.04	0.82	0.56
	2016	58	91	**0.86**	43	3.66	0.88	0.67
Montréal-Sorel	2001	187	94	0.00	51	3.83	0.90	0.67
	2015	114	178	**23.46**	56	4.01	0.91	0.69
Saint-Louis Lake	1997	46	81	0.00	35	2.95	0.75	0.57
	2005	100	156	0.00	38	2.93	0.76	0.56
	2011	100	76	**15.57**	41	3.73	0.89	0.70
Saint-François Lake	1996	43	76	0.00	20	2.99	0.83	0.69
	2004	66	134	0.00	32	1.31	0.34	0.26
	2009	65	126	**29.62**	35	2.25	0.66	0.44
	2014	62	64	**39.47**	33	2.87	0.76	0.57

Lake Saint-Louis, the Montreal-Sorel sector, Lake Saint-Pierre and Bécancour-Batiscan sector (Figure 1). For each experimental unit considered (sector * year, n = 19), species richness (total number of species captured), Shannon diversity index (H), Simpson's dominance (1-D) and Pielou's evenness (J) were calculated. Impacts of goby on diversity metrics were assessed using repeated-measures one-way analysis of variance (repeated-measures ANOVA) using the metrics as response variables, goby presence as a binary explanatory variable (presence/absence) and sector as the repeated factor.

Changes in the native littoral fish species community before and after invasions were illustrated using a multivariate analysis. Abundances of fish species were expressed as mean CPUE by experimental unit. Round goby abundances were excluded from the species matrix defining the fish community, so changes in the community structure were not attributed to the sole presence of the goby (i.e. +1 species) but rather to alterations to the native component of the community. Association between littoral fish community abundance (response variable) and native predator abundances (explanatory variable) was analyzed using a redundant discriminant analysis (RDA), a variant of the canonical correlation analysis (CCA). RDA analysis was calculated using the "*vegan*" package (Oksanen et al. 2017) in R software version 3.4.0 (R Development Core Team 2008). As suggested by Legendre and Gallagher (2001), communities raw species' abundance were transformed to be suitable for RDA analyses. Hence, CPUE values were transformed using the Chord transformation (a method preserving Euclidian distance among sites) using the *decostand* function (method = "normalize") from the *vegan* R package. Very rare fish species (< 4 observations within the 19 experimental units) were excluded from analysis to avoid biasing the community structure. Selection of the best explanatory variables (predators) for RDA was conducted through automatic permutation tests of the ordination model (function *ordistep* within *vegan* package). Littoral species with the highest RDA loadings (> |0.10|) for one of the two first axes were identified as the community most influential species (i.e. discriminating factor) explaining the differences observed between the 19 experimental units considered. To test the influence of round goby on species assemblage, round goby abundance (seine samples) were included along selected explanatory variables (native predators) in a second RDA analysis.

We quantified round goby impacts on the most influential native littoral species and predator abundances along the St-Lawrence River using linear mixed-effect models. The models considered either the CPUE of native littoral species or predators as a response variable while goby presence was considered as a binary explanatory variable (presence/absence) and study sector as the random factor, for the control of non-independence of observations. Abundance data of native species were square root transformed to fit the normal distribution assumption. Linear mixed models were calculated using the function *lme* in the R package nlme (Pinheiro et al. 2018).

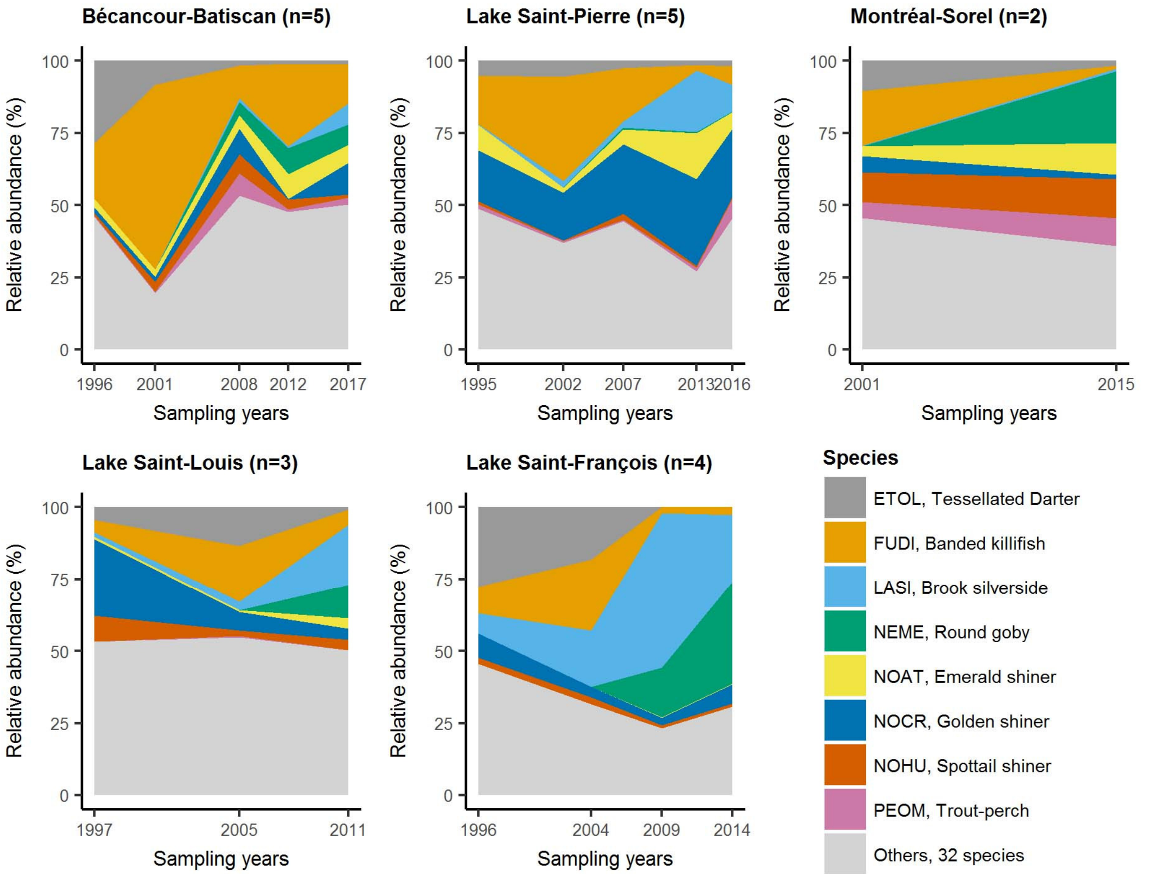

Figure 2. Change in relative abundance (% of total catch) in common species captured during the RSI surveys for each studied fluvial sectors (n = number of sampling years). Each color corresponds to a littoral fish species; named species are the most influential as identified by RDA analysis (see Results and Figure 3). Light gray areas are the other species (32 species). Round goby relative abundances in Lake St-Pierre are shown but represent about 1 % of total catch.

Results

After experiencing exponential demographic growth and range expansion in the 2000's, round goby abundance has recently stabilized (Figure 1). Since 2007, round goby occurred in 56% of all stations sampled using seine net. Although it is established throughout the river, the greatest abundances are observed in the upstream sectors of the St. Lawrence River. In Lake Saint-François, the density was on average 39.5 round goby per station in 2014 (2447 individuals at 62 stations, Table 1). In Lake Saint-Pierre, goby density decreased in recent years, passing from an average CPUE of 1.45 individuals in 2007 to 0.86 in 2016. Among the three most upstream sectors surveyed (Montréal-Sorel, Lake Saint-Louis and Lake Saint-François), round goby represented between 11.6 to 35.4% of all individual fish captured (Figure 2 and Supplementary material Table S1); it is now one of the most numerous of all 39 fishes captured by seine nets during the annual fish survey held in the St-Lawrence River. Interestingly, when considering the round goby as a component of the community matrix, species richness (N) increased in all sectors (repeated-measures ANOVA, $F_{1,13} = 17.81$, p = 0.001, Table 1). This relationship holds true when excluding round goby presence. However, the presence of round goby had no significant effect on any other littoral fish community diversity indices (repeated-measures ANOVA, $F_{1,13} = 0.16–2.21$, p-value = 0.16–0.70, Table 1).

Redundant discriminant analysis was calculated on normalized abundance data for 39 littoral species sampled in the five sectors (an additional 32 captured species were not included as less than 4 individuals were collected per species). The RDA model was globally significant (p = 0.004) and explained 32% of the constrained variance (adjusted $R^2 = 0.19$). The stepwise automatic RDA construction retained walleye,

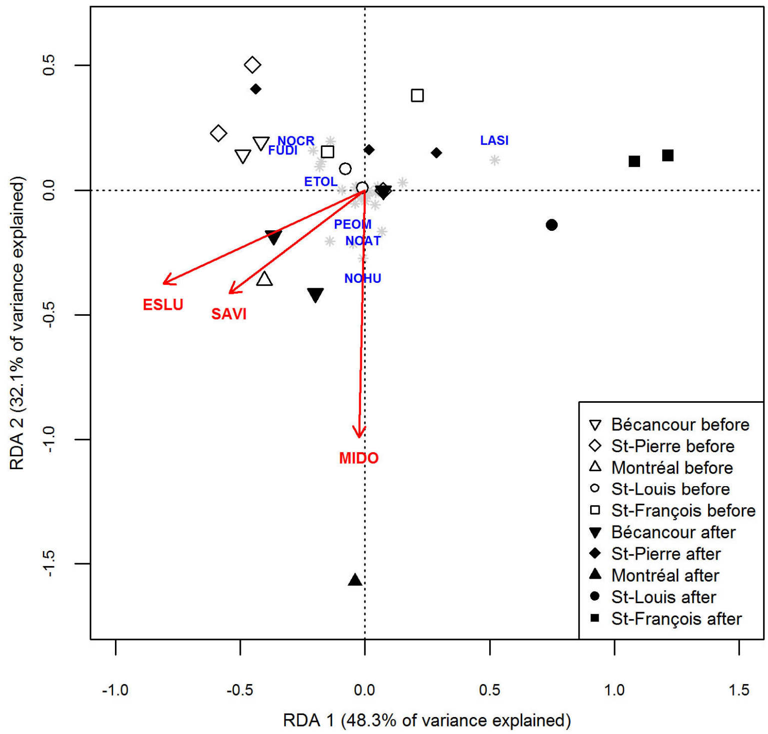

Figure 3. RDA of association between littoral fish communities and native predator abundances (red arrows, ESLU: northern pike, MIDO: smallmouth bass and SAVI: walleye) in lakes Saint-François, Saint-Louis, Saint-Pierre and the Bécancour-Batiscan and Montreal-Sorel stretches. Open symbols are community assemblages' position before round goby invasion and filled symbols are after round goby establishment. Gray stars are PCA species scores for 39 fish species in the analysis, most influential species in communities' dissimilarity are labelled, species codes are listed in Table 2.

Table 2. Species scores (loadings) of the two redundancy discriminant analysis axis, only the species with the highest loadings (positive or negative) are shown. Species codes are constituted of the two first letters of the genus and species scientific name.

Species	Common name	Species code	Loadings	
			RDA 1	RDA 2
L. sicculus	Brook silverside	LASI	0.52	0.12
N. hudsonius	Spottail shiner	NOHU	0.01	−0.21
P. omiscomaycus	Trout-perch	PEOM	−0.05	−0.22
N. atherinoides	Emerald shiner	NOAT	−0.14	−0.21
N. chrysoleucas	Golden shiner	NOCR	−0.14	0.20
E. olmstedi	Tessellated darter	ETOL	−0.18	0.16
F. diaphanus	Banded killifish	FUDI	−0.21	0.16

northern pike and smallmouth bass as the best explanatory variables. The first two RDA axes explained 81.3% of the ordination variance (Figure 3). Axis loadings (correlations) showed that seven species had loading values > |0.10| on at least one of the two axes (Table 2). The first RDA axis was mainly driven by brook silverside (*Labidesthes sicculus*) abundance and inversely correlated to the abundance of banded killifish (*Fundulus diaphanus*) and tessellated darter (*Etheostoma olmstedi*). The second RDA axis was dominated by the abundance of golden shiner (*Notemigonus crysoleucas*) and inversely correlated to the abundance of spottail shiner (*Notropis hudsonius*) and trout-perch (*Percopsis omiscomaycus*). Addition of round goby abundance as an explanatory variable did not significantly improve the percentage of variance explained by the model, although the round goby appears as an important explanatory variable (Figure S1, $p = 0.008$, 37.1% variance explained, adjusted $R^2 = 0.19$). Round goby abundance was inversely correlated to native predator abundance (Figure S1).

The linear mixed-models revealed that presence of round goby has a significant negative impact only on tessellated darter CPUE (Table 3). Conversely, we observed a positive effect on abundance of emerald shiner (*Notropis atherinoides*) and brook silverside CPUE (Table 3). The presence of round goby was generally associated with a decrease in CPUE of benthic littoral fish (darter and killifish) and with an increase in CPUE of small pelagic fish (Figure 4). Golden and spottail shiner decreased in abundance in Lake Saint-Louis but increased in all other sectors

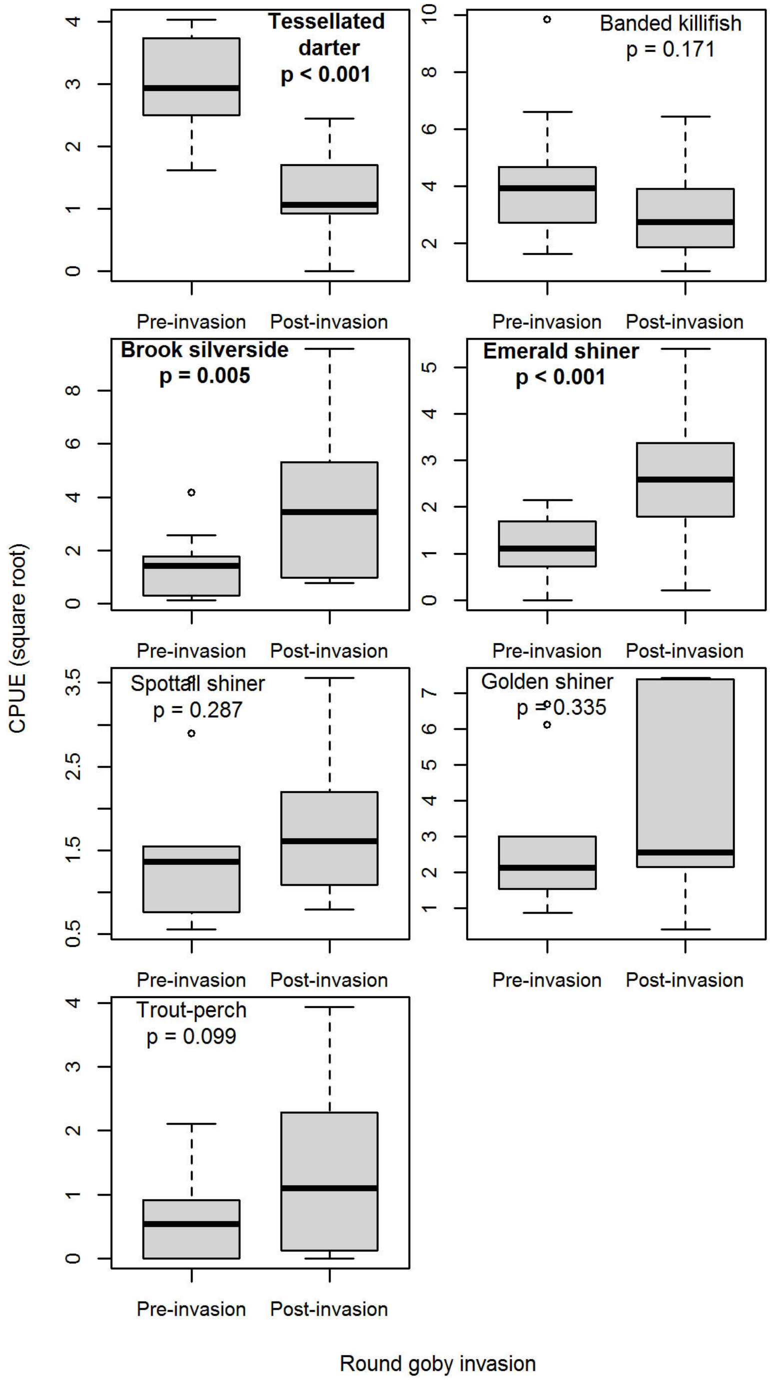

Figure 4. Catch per unit effort (CPUE, square root) of seven littoral fish species before and after round goby invasion. Bold species names are indicating significant effect of round goby presence on CPUE (see Table 3). Boxes are depicting interquartile range, median value is illustrated by the horizontal line, whiskers are showing data range (except outliers).

(Figure S2). For native predators, we observed a significant decrease in northern pike abundance after round goby invasion (Table 4). Although the average smallmouth bass abundance apparently increased following the establishment of the goby (Figure 5), the relationship was not significant at $\alpha = 0.05$. Trends in native predator abundance varied among the sectors studied (Figure S3). Smallmouth bass increased in abundance in all three fluvial lakes, but its abundance remained stable in the two riverine sectors (Montréal-Sorel and Bécancour-Batiscan; Figure S3). Finally, northern pike and walleye experienced an increase in the Lake Saint-Louis but declined in all other sectors (Figure S3).

Table 3. Linear mixed effects model for littoral fish species abundances (response variable, square root CPUE) in response of round goby invasion. Columns present the estimate of differences (positive or negative) in fish abundance with models intercept (abundance pre-invasion), standard error (SE), degree of freedom (df) and p-value, bold text indicate significant (p < 0.05) effect.

Coefficients	*Response* Estimate	SE	df	p-value
Tessellated darter				
Intercept	3.02	0.26	13	**< 0.001**
Post invasion	−1.84	0.35	13	**< 0.001**
Banded killifish				
Intercept	4.33	0.75	13	**< 0.001**
Post invasion	−1.36	0.94	13	0.17
Brook silverside				
Intercept	1.25	0.93	13	0.20
Post invasion	2.61	0.76	13	**0.005**
Emerald shiner				
Intercept	1.18	0.53	13	**0.04**
Post invasion	1.27	0.28	13	**< 0.001**
Golden shiner				
Intercept	2.75	0.99	13	**0.01**
Post invasion	0.67	0.67	13	0.34
Spottail shiner				
Intercept	1.64	0.43	13	**0.002**
Post invasion	0.34	0.31	13	0.29
Trout perch				
Intercept	0.77	0.47	13	0.13
Post invasion	0.64	0.36	13	0.10
Random parts				
N grp		5		
Observations		19		

Table 4. Linear mixed effects model for native predator fish species abundances (response variable, square root CPUE) in response of round goby invasion. Columns present the estimate of differences (positive or negative) in predators abundance with models intercept (abundance pre-invasion), standard error (SE), degree of freedom (df) and p-value, bold text indicate significant (p < 0.05) effect.

Coefficients	*Response* Estimate	SE	df	p-value
Northern pike				
Intercept	1.28	0.13	13	**< 0.001**
Post invasion	−0.68	0.17	13	**0.001**
Walleye				
Intercept	1.44	0.27	13	**< 0.001**
Post invasion	−0.16	0.18	13	0.39
Sauger				
Intercept	0.74	0.22	13	**0.006**
Post invasion	0.06	0.08	13	0.50
Smallmouth bass				
Intercept	0.62	0.13	13	**< 0.001**
Post invasion	0.28	0.14	13	0.07
Random parts				
N grp		5		
Observations		19		

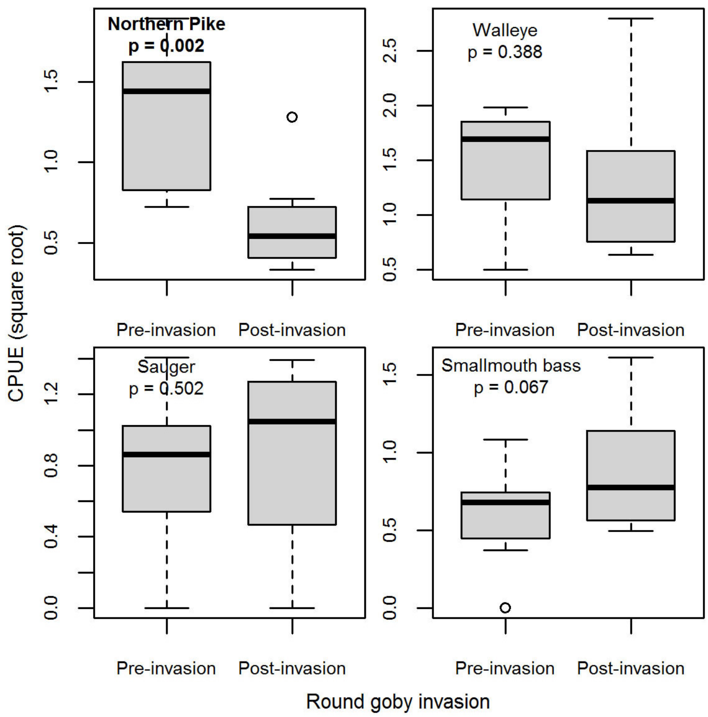

Figure 5. Catch per unit effort (CPUE, square root) of four native predator fish species before and after round goby invasion. Bold species names are indicating significant effect of round goby presence on CPUE (see Table 4). Boxes are depicting interquartile range, median value is illustrated by the horizontal line, whiskers are showing data range (except outliers).

Discussion

The impacts of round goby on the St. Lawrence River littoral fish community have been observed throughout the studied system. So far, 20 years after the first round goby capture in the St. Lawrence River, no species extirpation from the littoral fish community has been observed and species richness has not decreased in the five sectors studied. However, since its establishment, the round goby has nevertheless altered fish assemblages and has become one of the most (numerically) abundant species found in the littoral fish community. The littoral fish community experienced an important alteration in species abundance, notably through an increase in pelagic and demersal planktivorous fish and a reduction in small littoral benthic-feeders. This invasion was a major stressor for the St. Lawrence fish community, but certainly not the sole perturbing factor within the St. Lawrence River. For example, Lake Saint-Pierre yellow perch stocks were showing a steady decline well before the round goby invasion (Mailhot and Dumont 2003). This stock collapse has been associated with the combined effects of habitat degradation, increasing mortality rate (mainly by fisheries) and recruitment failure (Mailhot et al. 2015).

Tessellated darter populations have consistently declined since round goby establishment in the St. Lawrence River. Dietary competition (French and Jude 2001; Janssen and Jude 2001) between these two benthic species is a probable cause for the decline. This relationship is not fortuitous and should be considered as a supporting, albeit indirect, evidence that round goby can take over the ecological niche previously held by the tessellated darter. Round goby have been mainly described as a competitor to darters throughout the Great Lakes regions (Barton et al. 2005; French and Jude 2001; Lauer et al. 2004). All small benthic species sharing niche similarity with round goby are likely to be negatively impacted. Unfortunately, long-term survival in the St. Lawrence River of two species at risk could be in jeopardy: the vulnerable channel darter (*Percina copelandi*) and the endangered eastern sand darter (*Ammocrypta pellucida*). The low observation frequency (respectively 59 and 29 specimens in 20 years of RSI surveys) of those species preclude rigorous monitoring of their population abundance and assessment of the impacts generated by the round goby invasion. Moreover, in the Great Lakes, sculpins (*Cottus* spp.) and madtom (*Noturus* spp.) have been severely impacted by the round goby (Bergstrom and Mensinger 2009; Janssen and Jude 2001; Lauer et al. 2004). Unfortunately, those species are not frequently observed in RSI surveys (8 observations of mottled sculpin in 20 years). Hence, it is unclear if those species are in low abundance in the St. Lawrence River or not efficiently sampled by RSI survey gears. Hence, no conclusions concerning those species could be realized with the available data.

Simultaneous with the decrease in abundance of some species following round goby establishment, small pelagic and demersal fishes have consistently increased in abundance. The positive effects on brook silverside and emerald shiner (and to some extent on spottail and golden shiner) are consistent with the increase in golden shiner observed in Lake Huron (Riley et al. 2008). Direct competitive interactions with round goby are highly unlikely as small demersal/pelagic planktivores exploit distinct habitats and forage for different food items (Etnier and Starnes 1994; Johnson et al. 2017). This phenomenon may be seen as an indirect consequence of predation pressure relaxation, in the present case shifting the predation pressure on pelagic planktivores toward the benthic round goby. For example, Johnson et al. (2015) showed that diet of double-crested cormorant along the St. Lawrence River switched from being dominated by yellow perch (46%, by numbers) prior to the invasion to be dominated by round goby (49%) afterward; the yellow perch contribution to gut content dropping to 19% on average for the three birds colonies surveyed. Coincidently, cormorant abundances have drastically increased since the mid-2000s along the St. Lawrence River (Bédard et al. 1995; Johnson et al. 2015). Moreover, round goby has become an important prey for several piscivorous species, such as sauger, smallmouth bass and yellow perch (Reyjol et al. 2010). Gut content analyses of predators from the St. Lawrence River revealed that round goby was the only prey item found in stomachs for 21% to 64% of individuals and an additional 6 to 14% of fish had round goby along with other species in their guts (Reyjol et al. 2010). A similar observation was reported in the Bay of Quinte (Lake Ontario) where round goby were present in more than 80% of the stomachs of yellow perch and walleye; local abundance of goby was estimated between 5.0 to 11.2 tonnes/km^2 (Taraborelli et al. 2010). We believe that the negative effect of round goby presence on northern pike abundance is circumstantial rather than reflecting a causal relationship for this predator. Northern pike populations have reduced in abundance throughout the St. Lawrence River, with the notable exception of Lake Saint-Louis, as a result of the combined effect of overharvesting, constraining access to their high-quality spawning habitat and to the general degradation of the floodplain (Le Pichon et al. 2018). This situation was exacerbated in Lake Saint-Pierre where pike fisheries collapsed in the early 2000. The general demise of northern pike started before the arrival of the goby in the system. Today, one of the most abundant top predators in Lakes Saint-François, Saint-Louis and the Montreal-Sorel sector is the smallmouth bass. This new reality is similar to the changing food web dynamics and species interactions observed in Lake Erie, where round goby is now the dominant prey for smallmouth bass (observed in > 70% of fish). Goby presence has been demonstrated to be the cause of the 10 to 15% increase in the length-at-age of smallmouth bass between age 2 and 4 (Crane and Einhouse 2016).

Despite elevated local goby abundance, not all predators are actively feeding on them. Large predators, such as northern pike and walleye, feed heavily on round goby during their juvenile stages, however as they increase in size, predators shift their feeding preferences toward other species with higher energy content (Brodeur et al. 2011; Reyjol et al. 2010). Round goby possess a lower than average energy density (3.2 kJ/g) relative to clupeids, rainbow smelt and cyprinids (average = 5 kJ/g) (Kershner 1998; Ruetz III et al. 2009). The establishment of large populations of round goby in Lake Saint-Louis coincides with the increasing abundance of cohorts of sauger, walleye, yellow perch, smallmouth bass and northern pike reported in recent years by the RSI surveys and angling statistics (Gouvernement du Québec 2017). Whether this is a consequence of the new opportunity to feed on locally abundant goby or the result of recent management initiatives aimed at restoring stock abundance (instauration of a minimal and maximum harvest-length; Gouvernement du Québec 2017) remains to be assessed.

In Lake Saint-Pierre, Brodeur et al. (2011) showed that gobies were mainly predated by sauger, walleye and northern pike. The authors hypothesized that round goby would have a lower impact on Lake Saint-Pierre fish community structure as a consequence of predator-mediated effects on goby abundance, especially attributed to sauger, an abundant exclusively benthic predator (Lapointe et al. 2007; Ray and Corkum 2001). Accordingly, round goby abundance increased throughout the St. Lawrence River but local density observed in Lake Saint-Pierre always remained relatively low (mean = 1.02 goby CPUE) compared to the four other sectors (mean = 27.03 goby CPUE). Interestingly, despite this low goby abundance in Lake Saint-Pierre, small benthic fishes are nevertheless showing the same local abundance trend as all other sectors. This gives insight into the probable weak impacts of predator-mediated effects on native community. In Lake Saint-Louis, which is the only lake where all predators are abundant and growing (Figure S3), changes in littoral community were marginally different than elsewhere (e.g. shiner abundance), again, showing the potentially low contribution of predation pressure as an agent of impact mitigation.

The low abundances reported for the goby in Lake Saint-Pierre may also be related to an underestimation of *in situ* round goby densities as a consequence of the sampling gears used (e.g. seine nets) and the type of sampled habitats. Round goby reaches its highest densities on rocky substrate habitats (Ray and Corkum 2001), where seine could be suboptimal in efficiency. However, as the seine net has been used systematically in all sectors surveyed, we believed the lower goby abundance observed in Lake Saint-Pierre is not only linked to gear efficiency. High numbers of round goby have also been captured on sandy or muddy vegetated shoals in all sampled fluvial lakes (i.e. Saint-Louis and Saint-François). This is consistent with the observations that goby can reach similar densities between soft and hard substrata (Johnson et al. 2005a; Taraborelli et al. 2009). But, as rocky substrate is essential for round goby to complete their life-cycle (Kornis et al. 2012) their complete absence may impede their colonization opportunities. Lake St. Pierre, typified by vast muddy shoals covered by aquatic vegetation and very low abundance of hard substrata may be the least favourable habitat in the St. Lawrence system. We suggest that the low densities of goby in Lake Saint-Pierre may be more associated with the combination of largely unsuitable habitat and elevated predator pressure.

Implications for management

The capacity to keep track of fish community composition, and not only AIS density and dispersal, appears fundamental for quantifying impacts of AIS. In less than 10 years since the original detection in St. Lawrence River, the round goby has spread throughout the system and now represents an important component of the littoral fish community. Despite these observations, indices commonly used to illustrate impacts of AIS, such as biodiversity indices and species extirpation did not yield significant results nor expose the impacts of round goby on the St. Lawrence River ecosystem. It is only through the establishment, 20 years ago, of an annual standardized governmental fish survey that fish community changes following round goby invasion were quantified. Since goby has seemingly reached a near equilibrium status in the St. Lawrence River, a situation observed also in the Great Lakes (Kornis et al. 2012; Young et al. 2010), hope remains that goby's impacts on rare species, such as the channel and eastern sand darters, will not lead to local extirpation.

Along with prevention, preserving ecosystem capacity to withstand invasions should be considered a potential strategy toward establishing a precautionary approach for dealing with AIS. Biotic resistance to invasion has been identified as a key contributor limiting or controlling the spread of AIS (deRivera et al. 2005). Although the potential for predators to mitigate impacts of AIS may seem possible in some sectors of the St-Lawrence River, it needs to be further tested. While managing predators for preventing AIS invasion and spread may seem appealing, its practicality as a management tool needs to be fully assessed beyond theoretical considerations.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. RDA of association between littoral fish communities and native predator and round goby abundances in lakes Saint-François, Saint-Louis, Saint-Pierre and the Bécancour-Batiscan and Montreal-Sorel stretches.

Figure S2. Littoral fish species abundances (CPUE) before and after round goby invasion in fluvial sector Lake St. Louis, Lake St. François, Montréal-Sorel, Lake St. Pierre and Bécancour-Batiscan.

Figure S3. Native predators abundances (CPUE) before and after round goby invasion in fluvial sector Lake St. Louis, Lake St. François, Montréal-Sorel, Lake St. Pierre and Bécancour-Batiscan.

Table S1. Mean abundance (catch per unit effort) of the seven littoral species and round goby throughout the studied sectors.

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