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SCHOLARONE™ Manuscripts Spatial organization of fish communities in the St. Lawrence River: a test for the River Continuum and Serial Discontinuity Concepts in a large river system<sup>†</sup>

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# **Summary**

Typified by heterogeneous habitats, large rivers host diversified communities throughout their course. As the spatial organization of fish communities within these ecosystems remains little studied, concepts such as the River Continuum Concept (RCC) and the Serial Discontinuity Concept (SDC) were tested in the large temperate St. Lawrence River, Canada. We used a dataset from governmental standardized fish surveys (1995-2012) consisting of a total of 299 662 individuals from 76 fish species captured in 1 051 sites targeting two distinct communities: the littoral (nearshore) and pelagic (midshore). Results from diversity indices and multivariate analyses revealed a gradual downstream increase in taxonomic diversity as predicted by the RCC, and a gradual change of the community structure along the river. In addition, we observed different fish communities within fluvial lakes and corridor sectors as predicted by the SDC and found significant differences in fish community structure along opposite shores. The pelagic community changes more gradually along the river than the littoral community, likely as a combined result of a higher portion of more mobile fish species and the fact that pelagic habitats are less fragmented. The structure and organisation of fish communities along the St. Lawrence River stresses the need to better understand how biodiversity is distributed over large spatial scales, especially if science-based policies and actions are implemented toward preserving and restoring large systems where prioritization had to be made.

### **Introduction**

Large rivers are composed of a mosaic of habitats supporting diversified communities of plants and animals. Landscape heterogeneity, as well as environmental conditions and disturbances, are recognized as primary forces shaping the spatial distribution of fish communities (Robinson, Tockner & Ward, 2002; Ward *et al.*, 2002; Nilsson *et al.*, 2005). Albeit widely studied in streams and small to medium-size rivers (Pekárik *et al.*, 2011; Suvarnaraksha *et al.*, 2012; Konan *et al.*, 2015), only a few studies have targeted large rivers, perhaps due to the sheer size of those systems and the lack of large scale standardised surveys. Large rivers are distinguished from medium-sized rivers as the former's mean annual discharge exceed 7 500 m<sup>3</sup>•s<sup>-1</sup> and their watershed is larger than 900 000 km<sup>2</sup> (Bethemont, 2003).

The River Continuum Concept (RCC; Vannote *et al.*, 1980) describes rivers as a longitudinal gradient of environmental conditions shaping the distribution and organization of communities from the depauperate headwaters to the diversified river mouth. The RCC predicts a gradual downstream increase in species richness. This pattern was confirmed by several studies targeting small to medium-size rivers (e.g. Belliard, Boët & Tales, 1997; Araûjo, Pinto & Teixeira, 2009; Wu *et al.*, 2011; Kiraly *et al.*, 2015). Lowe-McConnell (1995) suggested that this upstream-downstream pattern is mainly driven by habitat diversity, which tends to increase from the headwaters to the river mouth.

In parallel, the Serial Discontinuity Concept (SDC; Ward & Stanford, 1983) predicts that natural and anthropogenic disruptions will lead to longitudinal discontinuities in biological organization at the population level (e.g. abundance), community (e.g. richness, dominance) or even at the ecosystem level (e.g. productivity). The SDC is a conceptual framework often used to explain the effects of dams, tributaries or geomorphological discontinuities on biological organization in

the river continuum (Hillbricht-Ilkowska, 1999; Stanford & Ward, 2001; Agostinho, Pelicice & Gomes, 2008). Dams have severely altered the natural hydrology, the habitats, and the connectivity within rivers (Johnson, Richardson & Naimo, 1995; Nilsson *et al.*, 2005; Liermann *et al.*, 2012) resulting in a reduction of local biodiversity while homogenizing fish communities (e.g. Mekong River; Li *et al.*, 2013). Moreover, Ward and Stanford (1995) expanded the SDC to include the floodplains dynamic that may result in transversal discontinuities impacting the spatial organization of the communities (i.e. channel-riparian gradient: Makrakis *et al.*, 2012; White, Ondrackova & Reichard, 2012). The presence of deep channels, where most of the water flows, and the distance separating the riverbanks of large rivers (frequently exceeding one km), may encompass pronounced gradients in biotic and abiotic conditions (e.g. current speed, temperature, depth, vegetation, etc.) that could act as potential transversal discontinuities. To our knowledge, the barriers that deep artificial channels may create between opposing shore communities have never been considered as a factor influencing the organization and differentiation of fish communities.

The main objective of this study is to test if the spatial organization of fish communities conforms to the theoretical expectations of the RCC and the SDC in a large temperate river. Specifically, we (1) characterized the organisation of fish communities along a longitudinal gradient in the St. Lawrence River and (2) identified potential longitudinal and transversal (i.e. between opposing shores) discontinuities. To fulfil these objectives, we analysed the fish community structure using a large data set covering two different habitats of the St. Lawrence River from Cornwall to Québec City (424 km stretch): the nearshore littoral community (located between 0 and 1.5 m deep) and the midshore pelagic community where pelagic species are found (located in water column ranging from 1 to 14 m). The portion studied is highly heterogeneous

both longitudinally and transversally due to the physical characteristics of the fluvial lakes alternating with narrow corridors, rapids, archipelagos, and the presence of a freshwater tidal zone in the downstream portion. The SDC predicts that fish community structure should respond to discontinuities generated by natural fluvial lakes and man-made barriers (e.g. dams and artificial channels). We also predict that fish communities may respond differently to the expectations of the RCC and SDC according to their habitat preferences and the swimming capacity of the component species. Fish communities exploiting the midshore water column (pelagic habitats) are expected to be less impacted by spatial discontinuities than communities exploiting shallow habitats located nearshore (littoral habitats).

#### Methods

#### Study area

The St. Lawrence River is one of the largest rivers in the world, both in terms of watershed area (1 344 200 km²) and mean annual discharge (12 600 m³•s⁻¹ at Québec city; Morin & Bouchard, 2000). The St. Lawrence River drains the North American Great Lakes, which contains more than 20% of all freshwater reserves of the world. The 550 km freshwater portion of the river, from the lake Ontario outlet to Québec City (Fig. 1), is generally shallow (<3 m) except for an artificially maintained navigation channel that divides the river transversally (the St. Lawrence Seaway; width  $\geq$  300 m; depth  $\geq$  11.3 m downstream Montréal harbour and  $\geq$  8.2 m upstream Montréal; mean current velocity of 0.5-2.0 m•s⁻¹). Most of water flow occurs in the navigation channel (up to 90%) and no water exchanges occur between the north and south shores upstream of Trois-Rivières (i.e. the beginning of the tidal freshwater-fluvial estuary). The uninterrupted freshwater river section (350 km) of the St. Lawrence River spans from the Beauharnois dam

downstream to the middle estuary where it continues uninterrupted to the sea (Fig. 1). In our study site, only Lake Saint-François is located upstream of the Beauharnois dam and downstream of the Moses-Saunders dam. Lake Saint-François water level is fully stabilized and it's water flow regulated by the two dams operated for hydroelectric power production (Morin *et al.*, 2000; La Violette, 2004).

A total of 97 freshwater and diadromous fish species, including 9 non-native species, are known to exploit the St. Lawrence River (MFFP data bases). Compared to similar large temperate rivers, fish richness in the St. Lawrence River is high and comparable to Mississippi River (102 species), while it is more diversified that Volga (63 species) or Danube (58 species; Galat, 2001 and the references therein). The high diversity observed in the St. Lawrence River may result from the combination of the inland post-glacial recolonization routes following the Wisconsinan glaciation to the natural connectivity with the Atlantic coast through the Gulf of St. Lawrence (Legendre & Legendre, 1984; Lacasse & Magnan, 1994).

#### The standardized fish survey

The standardized governmental fish survey in the St. Lawrence River, known as the RSI ("Réseau de Suivi Ichtyologique", described in La Violette *et al.*, 2003), characterizes the fish community structure at the end of the growing season (August to October). The whole river is divided in seven different areas (hereafter called sectors) according to their specific hydrological and morphometric characteristics. We thus recognize (Fig. 1) three distinct fluvial lakes; (1) Lake Saint-François (LSF; width: 7 km, length: 27 km), (2) Lake Saint-Louis (LSL; width: 11 km, length: 18.5 km), and (3) Lake Saint-Pierre (LSP; width: 12.8 km, length: 25.6 km), (4) an archipelago called Lake Saint-Pierre Archipelago (A-LSP; width: 10.5 km, length: 22.4 km)

and three narrower corridor sections including (5) Montréal-Sorel (MS; width: 3 km, length: 46 km), (6) Bécancour-Batiscan (BB; width: 3 km, length: 28 km), and (7) Grondines-Saint-Nicolas (GSN; width: 3 km, length: 55 km). Although the last two sectors are contiguous, they are considered separately as Grondines marks the beginning of mesotidal portion of the fluvial estuary with average tidal amplitude of 1.8 m (Gauthier, 2000). The Lachine Rapids, south of Montréal, was not considered in the present study because the powerful hydrodynamic flow regime prevents the use of the standardized sampling surveys protocol.

Fish communities were sampled every one km using both a standard beach seine net (12.5 m long × 4 m deep and 3.2 mm stretched mesh) and 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, 15-28.5 hours fishing period; La Violette *et al.*, 2003). Seine and gillnet gears have been shown to be efficient in assessing fish community diversity in rivers and detecting changes in fish community structure (Leclerc, 1990; Argent & Kimmel, 2005; Ri & Gelwick, 2005; Lapointe, Corkum & Mandrak, 2006). Seine nets were preferred for sampling the fish community in nearshore littorals habitats (<1.5 m; hereafter referred to as the "littoral community"), while gillnets were used for sampling the deeper water column were pelagic species occurs (between 1 and 14 m; average of 6.2 m; hereafter referred to as the "pelagic community").

Because of the sheer size of the St. Lawrence, only one or two sectors were sampled yearly. From 1995 to 2012, all sectors were sampled three times, except for MS, GSN and BB that were sampled one, two and four times respectively. As we intend to assess fish biodiversity organization throughout the St. Lawrence River using the RSI data, in the present study, we restrained our analyses to the spatial variability. As temporal variability is key information much needed for management and for better understanding the evolution of communities in today's

world facing global changes, the temporal perspective will be assessed when a dataset spanning over a longer timeframe will be made available. Preliminary temporal analyses of the RSI database suggest that spatial patterns predominate over temporal scale over the 17 years covered by the RSI (Foubert *et al.*, unpubl. data), interestingly Chick *et al.* (2005) arrived to a similar conclusion for fish community collected in the Mississippi from 1994 to 2002. Thus, in the present study, we pooled samples from different years (i.e. temporal variability) to better represent the "average" community structure locally.

When considering both gears, a total of 1 051 sites were sampled one to four times over the 17 years period (total of 2 386 samples; see Appendix Table S1 in Supporting Information). A grand total of 519 sites were sampled using seine nets (total of 1 127 samples) and 532 sites were sampled using gillnets (total of 1 259 samples). In each sector, an average ( $\pm$  SD) of 74 ( $\pm$  34) sites were sampled with seine nets and 76 ( $\pm$  12) with gillnets. Both seine nets and gillnets sites were grouped within ecological segment (named hereafter segment) predefined by the ecological reference framework from the present Ministère du Développement Durable, de l'Environnement et de la Lutte contre les Changements Climatiques du Québec (DesGranges & Ducruc, 1998). The ecological segments were only defined by the shoreline morphology (i.e. based on specific shapes such as straight, sinuous, indented, "closed" or "open" bay). Finally, as the deep navigational channel is dividing the river in a northern and southern portion along its course, we analysed each shore separately for both littoral and pelagic samples. As such, individual segment includes samples collected along only one shore. The average number of sites per segment was 19 ( $\pm$  9) and 20 ( $\pm$  12) for the seine and gillnet respectively. Along the entire study area, a total of 63 segments were defined with an average of 9 ( $\pm$  1) segments per sector (Fig. 1; Table S1).

#### **Indices of diversity**

All diversity indices were estimated at the scale of the ecological segments with pooled sites/samples in each segment. The fish diversity was analysed using three complementary and robust indices. Firstly, the rarefaction index (ES<sub>n</sub>) of Hurlbert (1971) corresponds to the expected number of species identified from a random subsample; the subsample size was set to 70 individuals for the littoral community (ES<sub>70</sub>) and 30 individuals for the pelagic community (ES<sub>30</sub>). The rarefaction index allows the comparison of species richness from unequal sampling effort. A minimum of (n) 30 individuals is usually required for a good estimate of the rarefaction index (Gotelli & Colwell, 2001). This criterion was not met for only one segment of the pelagic community located in the Montréal-Sorel sector. Secondly, we calculated from the raw data the Simpson diversity (1- $\lambda$ ) that takes into account both species richness and abundance distribution. Thirdly, we used the average taxonomic distinctness ( $\Delta$ \*, that is the expected taxonomic distance to the order level apart from two individuals from different species chosen at random from the sample) to estimate the taxonomic "breadth" of an assemblage and the relatedness of its constituent species (Clarke & Warwick, 1998).

#### **Data analyses**

Testing the River Continuum Concept

Differences in diversity indices among sectors were tested, one at a time, using a non-parametric permutational multivariate analysis of variance (PERMANOVA, with 999 permutations; Anderson, Gorley & Clarke, 2008) with Euclidian distance matrix. PERMANOVA generates the null distribution of the test statistic without assumptions of normality (Fairclough *et al.*, 2008).

A multivariate seriation test (Index of Multivariate Seriation IMS; RELATE procedure with maximum 999 permutations with Bray-Curtis similarities) was used to determine if fish community structure changes gradually along the longitudinal axis of the river (Somerfield, Clarke & Olsgard, 2002; Clarke et al., 2014). Abundance data were log transformed to adjust the balance between the contributions of dominant and rarer species (Clarke, 1993). If community changes along the St. Lawrence conform to a stepping-stone model of variation (e.g. segment 1 is more similar to its neighbouring segments than distant segments while the amplitude of dissimilarity is correlated with distance), the correlation will be maximized and the index, IMS (Rho), would equal the highest value (=1). The seriations were separately analysed for two types of communities and shores.

Testing the Serial Discontinuity Concept

Differences Differences among fish community structure (log-transformed abundance, Bray-Curtis similarities) considering a series of factors (sectors, hydro-morphological units (fluvial lakes vs. corridors) and shores (north vs. south)), were investigated using PERMANOVA with 999 permutations. Due to small number of permutations for all treatments when comparing shores within sector, Monte Carlo p-values ( $p_{mc}$ ) were used (Anderson, Gorley & Clarke, 2008). Community structure discriminated according to the abovementioned factors was compared using a Principal Coordinate Analysis (PCoA; Anderson, Gorley & Clarke, 2008). The later was combined to an Indicator Species Analysis (IndVal; Dufrene & Legendre, 1997) that identify species significantly associated to the various factors considered in the PCoA (e.g. considering only the north shore littoral community, what are the species significantly associated to fluvial lakes vs. corridors vs. archipelago?). As the IndVal can identify indicative species only for

dichotomous contrasts (e.g. lakes vs. corridors), the presence of the third category in the form of the archipelago (A-LSP) requires the IndVal to be coupled to a multi-levels pattern analysis (De Cáceres, Legendre & Moretti, 2010; e.g. Casatti *et al.*, 2012). Significance was tested using a random permutation procedure (Dufrene & Legendre, 1997). The "Holm" adjustment method (Holm, 1979) was used to correct for multiple testing (De Cáceres, Legendre & Moretti, 2010). A simple IndVal analysis was also performed to identify indicator species of the overall pelagic vs. littoral community.

As data can be listed as a spatial sequence, the contiguity information can be used to identify discontinuities along the series (De'ath & Fabricius, 2000; Borcard, Gillet & Legendre, 2011). A multivariate regression tree (MRT) was used to identify discontinuities along the upstream-downstream gradient of the St. Lawrence River using log-transformed species abundance. The result is a tree whose "leaves" (terminal groups of segments) are made up of subsets of segments, which minimize the within-group sums of squares. The MRT were separately analysed for the two types of communities and shores.

All analyses were performed using PRIMER (version 6.1, Plymouth Marine Laboratory; Clarke & Gorley, 2006) and R functions (version 3.1.3; R Core Team, 2015) with mvpart function for the MRT analyses, multipatt function for the IndVal analyses and p.adjust function for the "Holm" adjustment method. A significant level of  $\alpha = 0.05$  was used for all statistical tests.

#### **Results**

#### Littoral and pelagic fish communities

The data set encompassed a total of 299 662 individual fish belonging to 76 species and 25 families (see Appendix Table S2 and S3 in Supporting Information). A total of 249 309 fish were

captured by seine nets in nearshore littoral habitats, while 50 353 fish were captured by gillnets in the midshore pelagic habitats. The two habitats supported species from distinct communities in all sectors of the St. Lawrence River (P = 0.001); 71 species belonging to 24 families were collected in the littoral community while 45 species belonging to 20 families were captured in the pelagic community. The number of species observed per sample varied from 0 to 26 species (mean  $\pm$  SD:  $8.3 \pm 4.6$ ) for littoral sites and 0 to 18 species ( $6.4 \pm 2.8$ ) for pelagic sites. The littoral community was composed of 27 indicator species, including several Cyprinids, whereas 10 species, including larger and more mobile fishes, such as *Acipenser fulvescens* and *Lota lota*, characterized the pelagic community (see Appendix Table S4 in Supporting Information).

# **Testing the River Continuum Concept**

Diversity indices

The average taxonomic distinctness among sectors for the littoral and the pelagic communities conforms to the predictions of the RCC (Fig. 2e and 2f). When excluding the GSN, the rarefaction index and Simpson diversity conforms to the predictions of the RCC for the pelagic community only (see Fig. 2b and 2d). Rarefaction indices appeared highly variable along the river for the littoral community (see Fig. 2a).

From upstream to downstream, the total number of species changed from 46 species in LSF, 58 in LSL, 52 in MS, 55 in A-LSP, 56 in LSP, 56 in BB and finally 37 in GSN (see Appendix Fig. S1 in Supporting Information). In LSF, all diversity indices for both littoral and pelagic communities were low (Fig. 2). Conversely, except for the average taxonomic distinctness in littoral habitat (Fig. 2e), the A-LSP exhibited high values of diversity. Illustrating the complementarity of information brought by the various indices, despite the fact that GSN

showed high average taxonomic distinctness values for both fish communities (Fig. 2e,f), GSN had lower values for rarefaction indices (i.e. expected richness for  $ES_{70}$  and  $ES_{30}$ , see methods) and Simpson diversity (1- $\lambda$ '). The LSL littoral community exhibited high values of rarefaction and Simpson indices (i.e. Fig. 2a, c) but not the pelagic community (Fig. 2b, d). For both communities, BB exhibited high values of three diversity indices while LSP and MS showed intermediate values.

#### IMS results

Results from the index of multivariate seriation (IMS) analysis support the predictions of the RCC as they revealed that fish communities gradually changed along the St. Lawrence River with a significant IMS trend (P < 0.007; see Appendix Fig. S2 in Supporting Information). Rho values indicating the strength of a gradual change along the upstream-downstream axis, were higher for pelagic (0.59) than for littoral communities (0.48) and higher for north shore (0.64 for both littoral and pelagic communities) than for south shore communities (0.43 for littoral and 0.56 for pelagic communities).

#### **Testing the Serial Discontinuity Concept**

Differences among sectors

Results support the SDC model as it identified discontinuities within the St. Lawrence fish communities that paralleled the system's heterogeneous hydro-morphologic characteristics. Every sector hosted significantly distinct fish communities (all pairwise P < 0.05; except between A-LSP and BB for the pelagic community where P = 0.12), while GSN appears as the most divergent sector (see Appendix Table S5 in Supporting Information). The elevated disparities

between sectors are also highlighted by the multivariate regression trees (MRT; Fig. 3 and Fig. 4). This later observation reinforces our belief that the St. Lawrence is highly heterogeneous at the sector level. Furthermore, the precision of the MRT analyses even suggest that the St. Lawrence may be subdivided differently depending on the community considered compared to the actual generalisation of the dichotomous lake vs. corridor sectors (Fig. 3). For example, the MRT identify a major break in the littoral community of northern LSP while such break is inexistent for the pelagic community (Fig. 4). On the other hand, different sectors appeared undifferentiated for some community such as the northern littoral community of the LSP that spawns downstream into the BB sector (Fig. 3).

Differences between hydro-morphological units

Fluvial lakes (LSF, LSL and LSP), corridors (MS, BB and GSN) and the archipelago (A-LSP) are home to different fish communities. There were significant differences between hydromorphological units for both the littoral (PERMANOVA; Pseudo- $F_{2;55}$ =8.2; all P<0.004) and the pelagic community structures (Pseudo- $F_{2;60}$ =10.6; all P<0.02). These differences were also identified in the PCoA ordination plots (Fig. 5).

In fluvial lakes, four indicator species were identified for the littoral community (e.g. *Ameiurus nebulosus* and *Notemigonus crysoleucas*) and seven for the pelagic community (e.g. *Perca flavescens* and *Lepomis gibbosus*). In corridors, four species were also indicators of the littoral community (e.g. *Alosa sapidissima* and *Percopsis omiscomaycus*) while none were found for pelagic community (Fig. 5). In the archipelago, 11 and 9 indicator species were identified for the littoral and the pelagic communities respectively. The smaller number of segments (n=8) present in the archipelago as likely biased upward the number of indicator species detected for this

unique sector. A total of 13 of the combined 21 indicator species identified for the archipelago were common with either the fluvial lakes (9) or the corridors (4).

The Bray-Curtis dissimilarity comparisons show that, for both communities, corridors segments are structurally more variable than fluvial lake segments (Fig. 6). This observation is supported by both (1) the non-overlapping confidence intervals between lakes and corridors and (2) the higher total variance of Bray-Curtis distances observed for the corridors segments (Fig. 6). The variability observed within the archipelago is difficult to judge, as only a few segments were available to calculate Bray-Curtis distances.

Differences between shores

The structure of fish communities was significantly different between shores in LSL, LSP and BB sectors for the littoral communities and in A-LSP, LSP and BB for the pelagic communities (all  $P_{\rm mc}$  <0.05).

### **Discussion**

Our results showed that hydro-morphologic characteristics and human disturbances (e.g. dams, navigational channel) have imprinted the spatial organization of the St. Lawrence River fish communities as predicted by the Serial Discontinuity Concept (SDC). Moreover, it appeared that despite longitudinal discontinuities, the taxonomic diversity pattern supported a downstream increase in accordance with the theoretical expectations developed in the River Continuum Concept (RCC).

The nature and sensitivity of the various diversity indices had to be considered toward their relevance in uncovering general assembly rules allowing support to the RCC and SDC. Highly

responsive indices to species abundance and the co-occurrence of congeneric species are quite useful in identifying significantly distinct fish communities and local processes, but are rather inadequate to shed light on large-scale patterns. As such, the taxonomic diversity index and multivariate analyses are illustrating the increase in the species diversity on solid assets; the longitudinal accretion of different species (e.g. distant families and generas) rather than a simple increase of ecologically-redundant congeneric species (e.g. cyprinids, centrarchids, etc.). Thus, we stresses that all indices are not equals and should be interpreted accordingly: robust indices (i.e. the average taxonomic distinctness) appear suitable in identifying large-scale process (e.g. RCC) but should be considered with precautions when identifying local process (e.g. local homogeneity, barriers, etc.), on the other hand, sensitive indices (i.e. the rarefaction index and Simpson diversity) are useful in detecting local process such as community breaks or in bringing support when searching for truly homogenous communities or barriers (e.g. SDC). As expected, the combination of complementary univariate and multivariate analyses of community characteristics greatly improved our ability to detect diversity patterns in a highly heterogeneous ecosystem (Clarke et al., 2014). The present study stresses the importance of analysing global patterns of diversity using robust diversity indices to avoid biasing estimates resulting from the gears used and sampling effort (Gotelli & Colwell, 2001) and to go beyond the overly simplistic view provided by considering the total number of species as an index describing the organisation of fish communities.

The Serial Discontinuity Concept for the St. Lawrence River

Longitudinal disruptions

Strong physical barriers created by dams are disrupting the continuum in the upstream portion of the St. Lawrence River in accordance with the predictions of the SDC. Indeed, the reduced fish diversity in the Lake Saint-François (LSF) and the distinct communities observed in the adjacent sector of Lake Saint-Louis (LSL) reflect the impacts of the physical isolation of the LSF created by the Moses-Saunders and the Beauharnois dams. It is clear that dams located on both sides of the LSF have created a distinct water body characterized by altered connectivity, stabilized water level and increased current velocity that most likely impacted the fish communities, including a reduced number of species (La Violette et al., 2003). In many rivers, including large systems, biodiversity observed close to dams is lower than downstream (Stanford & Ward, 2001; Nilsson et al., 2005; Santos, Albieri & Araujo, 2013; Holt et al., 2015). In the St. Lawrence, the magnitude of impacts caused by the Moses-Saunders and the Beauharnois dams on the continuum is difficult to evaluate as they are the only dams in the study area and they are located in the upstream portion of the system. Although 68 species, including native and exotics species, are observed upstream in lake Ontario (Crossman & Van Meter, 1979), only 37 fish species were captured in the LSF.

Contrasted hydro-morphological fluvial portions are an intrinsic characteristic of large rivers systems (Ashworth & Lewin, 2012). The natural variations in hydrology and geomorphologic characteristics along the St. Lawrence River imprint the structure of fish communities.

According to the SDC, contrasted hydro-geomorphological features along the river, such as the presence of a fluvial lake, may be seen as discontinuities along the continuum supporting different communities (e.g. plankton communities; Hillbricht-Ilkowska, 1999). Large fluvial lakes contain more shallow habitats than corridors sectors that are typified by deep habitats and high current velocity. Many species collected in fluvial lakes are limnophilic and vegetation-

dependant while species found in corridors are more rheophilic. Moreover, the corridors sectors in the St. Lawrence offered additional heterogeneous habitats; the MS corridor includes large islands whereas the more downstream sectors are influenced by tidal movement that gradually increases from BB to GSN. The mesotidal portion of the fluvial estuary, the GSN, is home to distinct fish communities compared to the upstream part of the St. Lawrence (seen also by Leclerc & DesGranges, 2005). Furthermore, the Lake Saint-Pierre Archipelago (A-LSP), composed of 103 islands and numerous channels (155 km of channels), hosts a distinct fish community contributing to longitudinal discontinuities and habitat heterogeneity in the St. Lawrence River. The fish community of the upstream part of the LSP appeared influenced by the A-LSP and the Maskinongé bay (identified as a productive habitat, Fig. 1), which contribute to fish community dissimilarities along north shore. More surprisingly, the downstream part of the LSP and the BB sector possess a similar littoral community suggesting a higher continuity that previously taught between the two sectors. Since the A-LSP and the LSP are areas considered highly productive, they had the potential to "export" surplus production downstream in sectors where emigrant fishes will eventually contribute homogenizing local communities.

# Transversal gradient

The large and deep navigation channel in the St. Lawrence River appears as a transversal physical discontinuity that impacts fish communities by impairing dispersal processes. Indeed, our results revealed differences between fish communities along north and south shores in the fluvial lakes and corridors. The local heterogeneity of habitats along each shore (e.g. watershed land use, hydro-geomorphology, tributaries etc.) and, in some areas, the large distance involved between opposing shores (e.g. up to 11 and 12.8 km in LSL and LSP respectively) may account

for the significant differences in fish communities between shores. Furthermore, the dominant land use in watershed and the water masses flowing along the north (suburban landscape, brown waters of the Ottawa tributary) and south (agricultural and industrial landscapes, green waters of the upper St. Lawrence) shores of the LSL are likely contributor to the perceived differences between northern and southern sector of the lake. Such differentiation between northern and southern shores exists along almost all along the course of the St. Lawrence. Downstream in the A-LSP, the southern sector is close to the navigation channel whereas the northern sector is made out of multiple islands and numerous small channels (see Fig. 1). In LSP, the Yamaska and Saint-François tributaries drains polluted waters into the southern region of LSP (MDDEP, 1998; Hudon & Carignan, 2008) which had deeply impacted the vegetation in southern LSP (an important loss of the underwater vegetation) but as the tributaries' waters did not cross the central navigation channel they had not impacted the northern part of LSP. Finally, the north shore of BB is largely artificialized while the south shore is composed of large vegetated shoals similar to what was the LSP until recently.

The differences observed between shores along the St. Lawrence River could also be useful to define new fish management units reflecting the observed heterogeneity of fish communities. Such differences were in fact observed in the genetic pattern of yellow perch (*Perca flavescens*) populations in the St. Lawrence River. Genetic discontinuities between the north and south shores of the LSL were associated to the sedentarity nature of these two populations (Leclerc *et al.*, 2008). Moreover, two sympatric populations of rainbow smelt (*Osmerus mordax*) found in the St. Lawrence Estuary were found to be spatially segregated along the north and south shores (Lecomte & Dodson, 2004; Dodson *et al.*, 2015).

# The River Continuum Concept for the St. Lawrence River

Longitudinal patterns

The taxonomic diversity patterns in the St. Lawrence River illustrate the importance of longitudinal connectivity in river systems where diversified sectors are not only the result of their intrinsic properties but also the result of their position along the continuum. The taxonomic diversity, a measure that integrates the phylogenetic hierarchy of fish communities, revealed a gradual downstream increase for both littoral and pelagic communities. This diversity pattern, as predicted by the RCC, cannot be solely attributed to an accumulation of species along the river. No sector is home to all species captured at the river scale and several species were only caught once (unique observation) in both upstream and downstream sectors (see Table S2 and S3). The increase of heterogeneity and naturalness in habitats from the headwater toward the river mouth would partly explain this diversity pattern. Firstly, the isolation of the Lake Saint-François (LSF) located between the Moses-Saunders and Beauharnois dams explained the low specific and taxonomic diversity seen upstream. The hydrological alterations related to the water regulation decreased downstream. Secondly, the complex mosaic of habitats in the Lake Saint-Pierre Archipelago (A-LSP) increases the specific diversity in the middle part of the St. Lawrence. The A-LSP hosts the richest (in rarefaction values) and the most diversified (in Simpson diversity values) fish communities. However, the low taxonomic distinctness value for the littoral communities in the A-LSP compared to downstream Bécancour-Batiscan (BB) and Grondines-Saint-Nicolas (GSN) sectors suggests a certain redundancy in fish species (i.e. congeneric species). Thirdly, downstream sectors, marking the beginning of the mesotidal portion of the fluvial estuary, are composed of fluvial and estuarine species (e.g. Dorosoma cepedianum, Microgadus tomcod; Gasterosteus aculeatus) due to its position along the longitudinal gradient.

While only a few species were captured in GSN, the local diversity is nevertheless important thanks to the average taxonomic difference existing between constituent species. Such observation is associated with (1) the smaller number of congeneric species found locally for species families (i.e. Centrarchidae, Cyprinidae) and (2) the simultaneous presence of species from the upper freshwater portion of the river together with estuarine / euryhaline species from the estuary bringing together distantly related species. Taken together it appears that spatial structure of fish communities gradually changed along the longitudinal gradient of the river, however, this result is not a mere steadily accumulation of species but appears rather as a combination of increasing geographical distance and cumulative riverscape heterogeneity along the continuum which increase the dissimilarity between upstream and downstream fish communities.

## *Unexpected diversity pattern*

While considering the general spatial pattern of diversity, we identified two sectors exhibiting levels either much higher (i.e. BB) or lower (i.e. LSP) than previously thought. Rarely considered as a hotspot for diversity, the little studied downstream Bécancour-Batiscan (BB) sector exhibits high values of rarefaction, Simpson diversity and taxonomic distinctness for both littoral and pelagic fish communities (Fig.2). The BB is located downstream of the Lake Saint-Pierre (LSP), with large vegetated shoals along the southern shore. These results emphasize the importance of better describing this sector in the eventuality of formulating plans to protect its biodiversity. In contrast, elevated values for fish diversity indices were expected for the LSP thanks to the sheer size of the area and the diversity of fish habitats it contains. The LSP is an extensive marshland due to its shallow topography (mean depth 2.7 m, maximum depth 13.7 m;

Carignan & Lorrain, 2000) with ubiquitous macrophyte beds and large floodplains generated during spring freshets (up to 54 500 ha; Richard *et al.*, 2011). However, the values of rarefaction, Simpson diversity and taxonomic distinctness of the littoral community of the LSP were, on average, similar to values reported elsewhere along the St. Lawrence River. Cumulative human pressures in the LSP may partly explain this pattern. For example, the advent of intensive agricultural practices (e.g. corn and soy) on the LSP floodplains has been identified as a primary cause for the collapse of the once locally super-abundant yellow perch (de la Chenelière, Brodeur & Mingelbier, 2014).

In addition, specific and taxonomic diversity indices revealed different hotspots along the St. Lawrence River (e.g. A-LSP and GSN sectors). Since taxonomic diversity considers the evolutionary relationships within fish communities, it explicitly incorporates species differences rather than just the number of species. Recognizing the difficulties associated to decision-making when prioritizing which areas should be protected in the face of limited financial resources, we argue that protecting the greatest number of species possible is not necessarily the most rewarding action; the taxonomic richness appears as a measure worth further considerations (Vellend *et al.*, 2011). In the St. Lawrence, while the number of fish families observed in the A-LSP is higher than in the GSN sector, the elevated number of congeneric species in the A-LSP (i.e. Cyprinidae, Centrarchidae and Percidae; see Table S1 and Table S2) lowers the value of the taxonomic diversity. For this reason, a higher taxonomical fish diversity is observed in the GSN sector for a similar number of species caught.

#### Littoral versus pelagic communities

The observed variability in the pelagic and littoral fish communities is consistent with the predictions of both the RCC and SDC concepts. In the St. Lawrence River, the large-scale diversity pattern from the pelagic community fits better the theoretical expectations of RCC as the various indices showed a smoother change along the longitudinal axis than for the littoral community (Fig. 2) and a sequential clustering supporting the upstream-downstream ordination of communities (Fig. 4). The littoral community seems to be more heterogeneous along the river, especially in fluvial lakes. This is probably due to smaller and less mobile fishes (e.g. Fundulus diaphanous and Pimephales notatus) in the littoral than the pelagic communities (e.g. with large and mobile Sander vitreum). Moreover, environmental forcing such as flooding together with human shore alterations may increase the landscape heterogeneity and fragmentation of littoral habitats. Inversely, the pelagic community exploits habitats more physically connected, where dispersal processes prevail (e.g. current velocity) in relation to species-specific traits (e.g. migratory, open-water species).

# The usefulness of large and standardized sampling program

Only the system-wide, multiannual and standardized surveys have allowed the detection of patterns within the fish community organisation along the St. Lawrence River. The RSI has captured to date almost a third of a million fishes, including rare species such as *Moxostoma* valenciennesi, Ammocrypta pellucida and Noturus flavus (see Table S2 and S3). However, the selectivity of gears used, the sampling period (e.g. some migratory species were not in the area at the moment of sampling) and the fact that some habitats were not sampled by the RSI (e.g. rapids, navigational channel) limits our ability to capture all species exploiting the St. Lawrence (i.e. 97 fish species) and accurately quantify densities for several species (e.g. Anguilla rostrata,

lampreys, alosines, salmons, carps). For example, whereas millions of *Anguilla rostrata* have migrated in the St. Lawrence, only two were found in our samples. While this dataset has already revealed key observations since 1995 (e.g. stocks collapse and spread of invasive species), we consider that the RSI reflects the abundance of the vast majority of species present in the system and allows depicting how communities are structured along the St. Lawrence.

#### **Concluding remarks**

This study illustrates the importance of longitudinal gradients in environmental conditions, riverscape heterogeneity and human disturbances in explaining variations in fish community diversity and structure in a large temperate river. The separation of littoral and pelagic communities in the analyses is a prerequisite to better understand how communities are structured, as both communities do not respond similarly to the same structuring factors. Our results illustrate that the River Continuum Concept (RCC) and the Serial Discontinuity Concept (SDC) are both relevant frameworks to better assess spatial organization of fish communities along the St. Lawrence River. The use of complementary diversity indices, both univariate and multivariate analyses, helped identifying longitudinal and discontinuities patterns along the river as predicted by both the RCC and SDC. These findings thus underline the importance of considering a set of different metrics and statistical approaches in the assessment of community-level biodiversity.

A better understanding of community architecture in a large river system allows determining geographical and ecological units for management and prioritizing sites to be protected, preserved or restored. Management units have to be based on the structure of fish communities taking into account ecological gradients and discontinuities (e.g. transversal differences between

the two shores). Even if hydro-morphological characteristics are useful to delineate functional management units, other elements or processes such as human disturbances and fish dispersal can influence the fish community organisation.



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# Figures legends

Figure 1: Map of the sectors studied (LSF, LSL, MS, A-LSP, LSP, BB and GSN) along the St. Lawrence River. The ecological segments and the navigation channel separating the shores are also shown. Note that for clarity the map was cut into 2 portions (upstream, upper part and downstream, lower part).

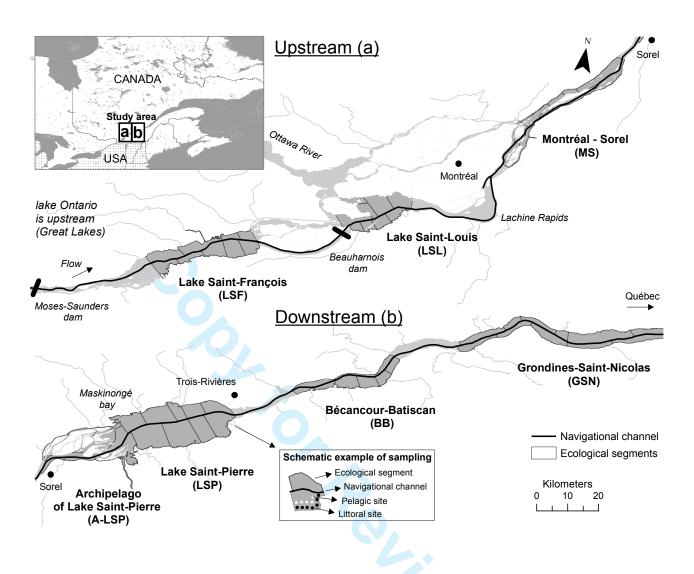
Figure 2: Point bars showing average values ( $\pm$  SE) of rarefaction index (ES<sub>30</sub> and ES<sub>70</sub> for pelagic and littoral communities respectively, see methods), Simpson diversity and taxonomic distinctness among sectors of the St. Lawrence River for littoral (graphs a, c, e) and pelagic (graphs b, d, f) fish communities. Sectors were ordered from upstream (left) to downstream (right). Different letters above bars represent significant differences (P < 0.05).

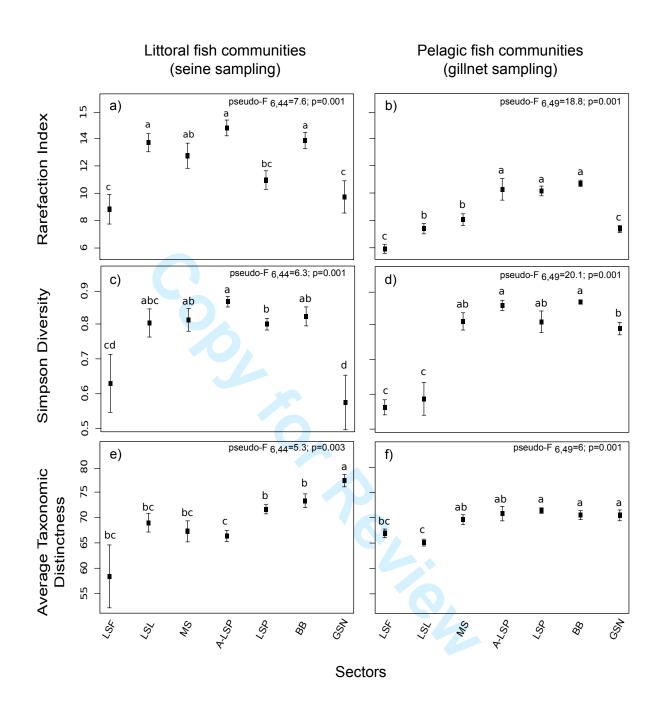
Figure 3: Discontinuities (dashed line) in *littoral fish communities* (with their node numbers) identified along the St. Lawrence River using a multivariate regression tree analysis (MRT). The navigation channel is used to separate the north from the south shore. For each leaf, the number of segments pooled are indicated. The tree explained 66% and 61.8% of the total sum of squares for the north and south shore respectively.

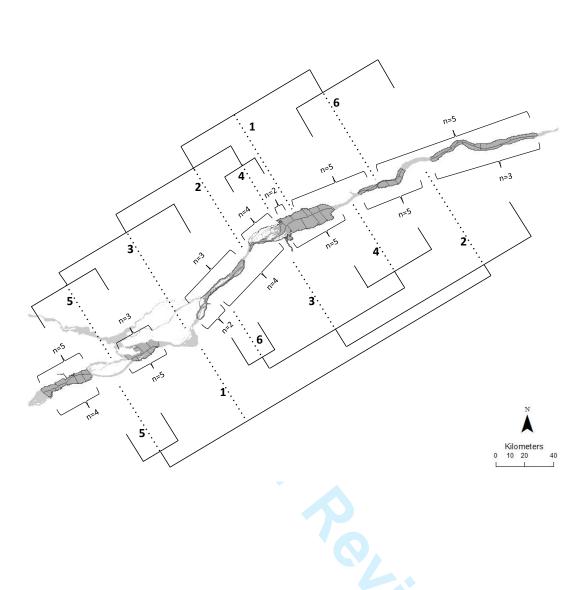
Figure 4: Discontinuities in *pelagic fish communities* identified using a multivariate regression tree analysis (MRT): see legend of Fig. 3. The tree explained 70.4% and 76.2% of the total sum of squares for the north and south shore respectively.

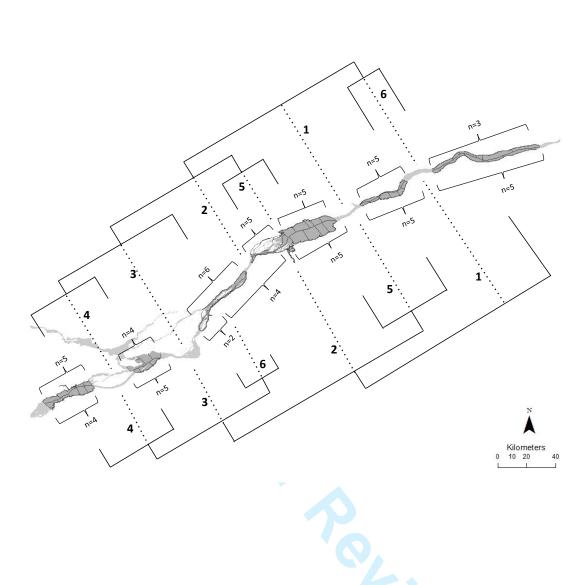
Figure 5: Principal Coordinate Analysis (PCoA) plots showing littoral (a, c) and pelagic (b, d) fish communities at the segment scale among sectors and shores. Indicator species abbreviations, that characterize fluvial lakes (black symbols), corridors (white symbols) and the archipelago (stars), are as follows: ALSA = *Alosa sapidissima*; AMCA = *Amia calva*; AMNE = *Ameiurus nebulosus*; ESLU = *Esox lucius*; ETNI = *Etheostoma nigrum*; HITE = *Hiodon tergisus*; HYRE = *Hybognathus regius*; LASI = *Labidesthes sicculus*; LEGI = *Lepomis gibbosus*; NOAT = *Notropis atherinoides*; NOCR = *Notemigonus crysoleucas*; NOHU = *Notropis hudsonius*; PEFL = *Perca flavescens*; PEOM = *Percopsis omiscomaycus*; PONI = *Pomoxis nigromaculatus*. The circle is a unit circle (radius = 1.0), whose position of origin (centre) corresponds to the centre of the plot (0,0). Each vector begins at the centre of the circle and ends at the coordinates (x, y) consisting of the Pearson correlations between indicator species and each of PCO axis 1 and 2, respectively. The length and direction of each vector indicates the strength and sign, respectively, of the relationship between indicator species and the PCO axes.

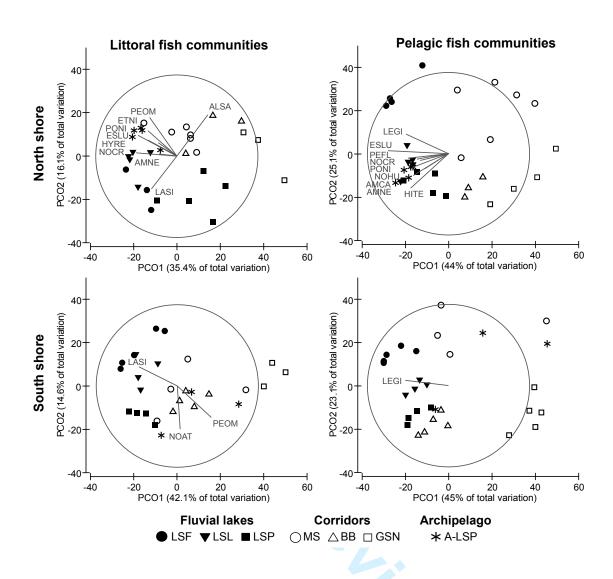
Figure 6: Point bars showing average values ( $\pm$  CI 95%) of Bray-Curtis dissimilarity between the littoral and the pelagic fish communities for the fluvial lakes, corridors and the archipelago of the St. Lawrence River. Numbers on the top correspond to the total variance of Bray-Curtis distances and numbers under the bar correspond to the total number of segments.

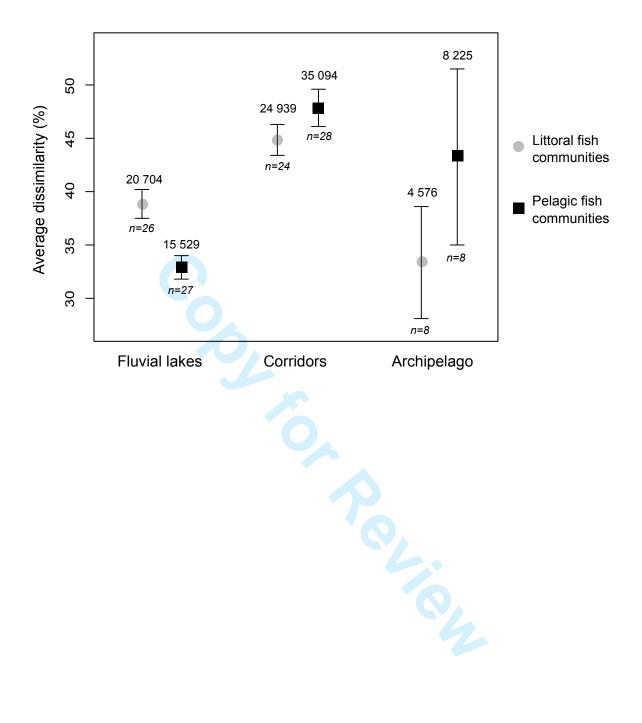












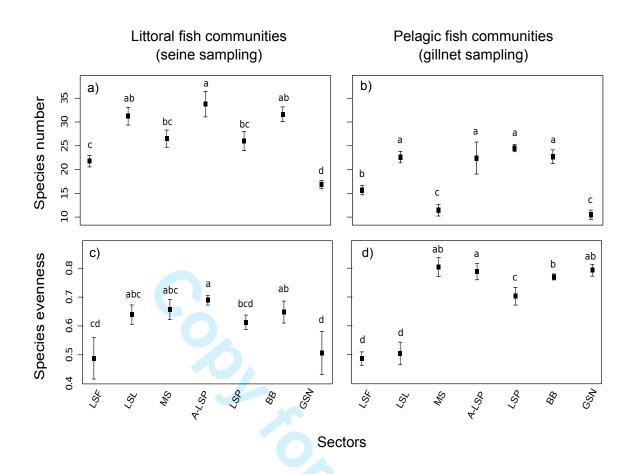


Figure S1: Point bars showing the average ( $\pm$  SE) of species richness (S) and species evenness (J') among sectors (upstream to downstream) of the St. Lawrence River for seine (graphs a, c) and gillnet (graphs b, d) samples. Different letters above bars represent significant differences (P < 0.05).

Except for A-LSP for both fish communities (average of richness for the littoral: 38 versus 26, and the pelagic fish communities: 27 vs 13, north and south respectively) and LSL for pelagic fish communities (24 vs 19 north and south respectively), no difference was observed between north and south shores (detailed average per sectors/shores not shown). These indices reveal a high variability for littoral and pelagic communities along the river. However, even if they are simple and informative, there are largely biased by the gears used and sampling effort.

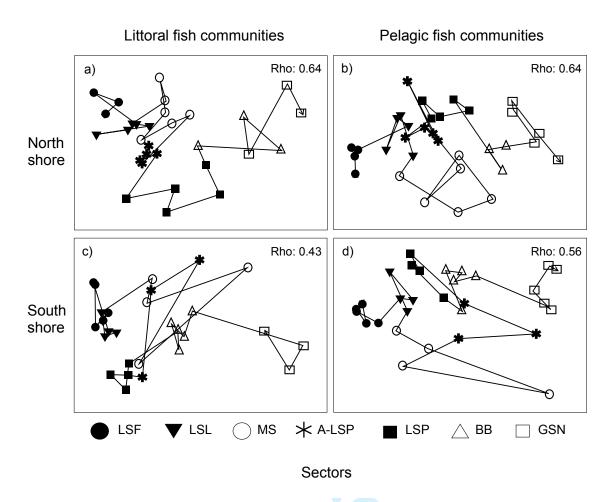


Figure S2: nMDS ordination plots representing sequential changes in segments of each sector of littoral (a, c) and pelagic (b, d) fish communities upstream to downstream along the north and south shores of the St. Lawrence River. The lines indicate successive segments along the river (upstream to downstream) within hydro-morphological units. Reading across rows, stress values = 0.15, 0.12, 0.14, 0.09.

The index of multivariate seriation (IMS; RELATE procedure in PRIMER) reveals that fish communities' changes along the St. Lawrence River is significant in all case  $(P \le 0.007)$  and follows a longitudinal gradient.

Table S1: Number of samples and number of sites targeted in each sector by the RSI ("Réseau de Suivi Ichtyologique") using the seine nets and gillnets. All sites were embedded in ecological segments dividing each sector.

SECTORS	Gears	Samples	Sites	Ecological segments
I also Saint François (I SE)	Seine nets	163	62	8
Lake Saint-François (LSF)	Gillnets	198	71	9
Laka Saint Lauis (LSL)	Seine nets	236	98	9
Lake Saint-Louis (LSL)	Gillnets	222	78	
Montrial Corol (MC)	Seine nets	115	115	10
Montréal-Sorel (MS)	Gillnets	79	79	
Archipelago of Lake Saint-	Seine nets	176	72	- 8
Pierre (A-LSP)	Gillnets	187	76	7 °
Lake Saint-Pierre (LSP)	Seine nets	155	63	9
	Gillnets	238	100	
Pagaragua Patingan (PP)	Seine nets	179	56	- 8
Becancour-Batiscan (BB)	Gillnets	231	64	7
Grondines-Saint-Nicolas	Seine nets	103	53	6
(GSN)	Gillnets	104	64	10
	Seine nets	1 127	519	
Total	Gillnets	1 259	532	63
	All	2 386	1,051	
		0	2	

Table S2: Average ( $\bar{x} \pm \text{SD}$ ) abundance of each species sampled by seine in the RSI from 1995 to 2012 in each sectors targeted of the St. Lawrence River. A total of 71 species from 24 families were collected. It appears that no sector is home to all species captured at the river scale.

		LSF		L	SL	MS		A-	LSP	ı	.SP	В	В	(	SSN	To	otal		
	Number of stations		163		2	36	1	115	1	.76		155	17	'9		103	1	127	
Ordre	Famillies	Species		x ± S	D	x.	± SD	x	± SD	x.	± SD	x	± SD	π±	SD	x	± SD	x	± SD
Acipenseriformes	Acipenseridae	Acipenser fulvescens	-		-	-	-		± 0.1	-	-	-	-	_	0.1	-	÷	_	± 0.7
Amiiformes	Amiidae	Amia calva	-		-	-	-		± 0.9		± 0.1	-	-	-	-	-	-	_	± 0.6
Anguilliformes	Anguillidae	Anguilla rostrata	-		-	_	± 0.9	- 0.4	- 2.5	- 1.0	- 7.2	-	- 12.0	-	- 1.0	-	-	_	± 0.4
Atheriniformes	Atherinopsidae	Labidesthes sicculus Alosa pseudoharengus	44.6 0.4	±	29.9 1.5	13.8 : 4.2 :	± 38.3 ± 25.3	_	± 2.5 ± 5.3	1.9 : 3.1 :			± 13.8 ± 1.5	0.5 ±			± 12.7	_	± 112.8 ± 13.2
Clupeiformes	Clupeidae	Alosa sapidissima	- 0.4	-	-	0.3		l	± 0.5	0.4		0.2		l	2.4	1.3		0.3	
olupello lilies	o.apc.aac	Dorosoma cepedianum	_		-	-	- 0.5	-	- 0.5	-		-	- 0.2	0.6 ±		0.2			± 0.5
		Catostomus catostomus	-		-	-	-	-	-	0.6	± 0.8	0.1	± 0.2	0.6 ±		_	± 0.4	0.2	
		Catostomus commersonii	0.2	±	0.8	0.3	± 0.9	2.9	± 1.2	2.0 :	± 4.2	0.2	± 0.8	1.7 ±	4.2	0.2	± 0.8	1.2	± 4.1
	Catostomidae	Carpiodes cyprinus	-		-	I .	± 0.7		± 1.6	0.4		-	-		1.5	-	-		± 1.4
	Catostonnaac	Moxostoma anisurum	0.4	±	0.3	0.5		0.6		0.6		0.1		0.5 ±		-	-	0.2	
		Moxostoma macrolepidotum	0.6	±	0.4	I .	± 0.4	l	± 11.1	2.6	± 4.5	0.3	± 1.8	1.3 ±	6.2	0.4	± 1.2		± 5.0
		Moxostoma valenciennesi Cyprinus carpio	-		-	_	± 0.7 ± 0.2	0.9	± 0.9 ± 1.0	0.3	- ± 0.8	0.5	± 0.2	0.2 ±	0.9	0.3	± 0.2		± 0.4 ± 0.6
		Cyprinella spiloptera	0.6	±	0.8	l	± 7.9	ı	± 12.4	0.5			± 1.5		1.7	-	1 0.2		± 5.8
		Exoglossum maxillingua	-	_	-	-	- 7.5	l	± 0.4	-	,	-	- 1.5	-		_	_		± 0.1
		Hybognathus regius	) -		-	-	-	l	± 4.7	29.4	± 264.9	0.2	± 1.4	0.8 ±	0.5	-	-		± 15.0
		Luxilus cornutus	-/		-	0.8	± 0.9	0.1	± 0.8	-	-	-	-	0.8 ±	0.6	-	-	0.3	± 0.3
		Notropis atherinoides	0.2	±	0.2	l	± 11.4	l	± 13.6	1	± 67.7	4.3		l	11.8	1.9	± 6.1		± 3.7
Cypriniformes		Notropis bifrenatus	0.2	±	2.3	l	± 3.7	ı	± 8.1	7.7		35.0		0.1 ±		-	-		± 35.7
		Notemigonus crysoleucas	3.6	±	14.9		± 39.4	l	± 33.4	23.4			± 77.0	2.5 ±		-	-		± 44.1
	Cyprinidae	Notropis heterodon Notropis heterolepis	0.8	±	4.7 0.3		± 8.2	0.9	± 0.9	0.2		1.6		0.1 ±		-	-		± 5.2
	Cyprinidae	Notropis hudsonius	1.7	±	5.2		± 56.7 ± 16.9	12.9	± 3.3	0.1 : 17.3 :		2.1	± 11.8 ± 3.6	l	9.0		± 1.5		± 26.3 ± 16.6
		Notropis rubellus	-	-	-		± 2.5	-	- 5.5	-	- 2.0		± 0.3	l	12.5	-			± 5.7
		Notropis stramineus	128.7	±	657.9		± 41.6	0.5	± 1.9	0.7 :	± 5.5	0.3		0.2 ±		-	_		± 254.2
		Notropis volucellus	179.7	± :	1299.4	37.2	± 348.4	33.2	± 166.6	1.9	± 28.8	3.8	± 19.8	3.2 ±	17.6	-	-	39.9	± 524.2
		Pimephales notatus	2.8	±	46.8	· ·	± 158.7	39.6	± 11.2	9.6	± 3.3	28.9	± 242.2	3.9 ±	12.8	1.0	± 1.0	24.8	± 124.2
		Pimephales promelas	-		-	0.4	± 0.7		-	-	-	0.6	± 0.8	0.3 ±	3.8	-	-		± 1.5
		Rhinichthys cataractae	-		-	-	-	-	-	0.6	± 0.8	-	-	-	-	0.3	± 0.3	1 '	± 0.9
		Semotilus atromaculatus	-		-	0.6	+ 0.4		± 0.9	0.2	- 0.1	0.1	- + 0.1	02 1	. 27	-	-		± 0.3
Cyprinodontiformes	Fundulidae	Semotilus corporalis Fundulus diaphanus	9.3	±	3.9		± 0.4 ± 2.5		± 0.2 ± 137.2	1.4	± 0.1 ± 6.6		± 0.1 ± 277.2		2.7	28.2	± 89.8	_	± 0.9 ± 122.5
сургиюшопиноппез	rundundae	Esox americanus americanus	-	<u> </u>	-	-	- 2.5	-	- 157.2	0.6		-	- 2//.2	-	- 65.0	-	- 05.0	_	± 0.3
F	Esocidae	Esox lucius	0.2	±	0.1	0.2	± 0.6	0.7	± 0.4	0.6		0.2	± 0.7	0.7 ±	0.3	0.2	± 0.1	0.2	
Esociformes		Esox masquinongy	0.2	±	0.1	0.2		0.1	± 0.5	0.6		-	-		0.2	-	-	0.2	± 0.3
	Umbridae	Umbra limi	-		-	_	± 0.7	-	/-/-		-	0.1	± 0.1	-	-	-	-	_	± 0.5
Gadiformes	Lotidae	Lota lota	-		-	0.4	± 0.7	-	-	-	-	-	-	-	-	-	-	_	± 0.3
C	C++-:-	Apeltes quadracus	-		-	-	-	-	. 0.7	-	-	-	-	0.1 ±		-	-	0.2	
Gasterosteiformes	Gasterosteidae	Culaea inconstans Gasterosteus aculeatus	-		-	0.3	± 2.7	0.1	± 0.7	7		-	-	0.4 ±	0.5	1.0	± 1.0	0.7	± 1.0 ± 0.4
Lepisosteiformes	Lepisosteidae	Lepisosteus osseus	-			0.3	± 0.2	0.5	± 0.6	0.6	± 0.8	0.6	± 0.8	0.6 ±		-	1 1.0	_	± 0.4 ± 0.2
Osmeriformes	Osmeridae	Osmerus mordax	0.6	±	0.8	_	± 0.7	_	± 1.1	0.3			± 0.8	_	2.8	1.0	± 0.5	_	± 1.3
Osteoglossiformes	Hiodontidae	Hiodon tergisus	-		-	-	-	_	± 1.4	_	± 0.6	7-	-	0.2 ±		0.1	± 1.2	0.9	± 0.7
		Ambloplites rupestris	2.8	±	6.5	7.8	± 12.3	6.8	± 14.8	5.4	± 1.9	0.6	± 2.4	0.4 ±	1.1	0.3	± 0.2	3.7	± 9.4
		Lepomis gibbosus	5.4	±	18.8	25.4		11.8	± 53.6	28.9	± 46.2	22.8	± 44.8	3.3 ±	24.8	0.2	± 0.1	15.5	
	Centrarchidae	Lepomis macrochirus	-			I .	± 0.7	-	-		-	-	-	-	-	-	-		± 0.3
		Micropterus dolomieu	0.2	±	0.4	0.3		0.7		0.4			± 0.2	l	0.9	0.5	± 1.6		± 1.9
		Micropterus salmoides Pomoxis nigromaculatus	1.3 0.2	±	3.3 1.4	1.7 : 1.3 :	± 3.9 ± 7.4	0.2 1.0		0.8 : 2.9 :			± 0.3 ± 0.5	0.6 ±	0.4	_	-		± 2.5 ± 4.5
	Gobiidae	Neogobius melanostomus	11.9		26.3		± 15.7	-		0.8			± 3.2		13.4	0.2	± 2.4	_	± 4.5 ± 14.1
		Morone americana	0.4	±	0.5	0.6		0.2		0.1		-	-		0.6		± 0.1	0.4	
	Moronidae	Morone saxatilis			-	-	_	-	-	-	-	-		l	0.1	-		0.2	± 0.6
Perciformes		Ammocrypta pellucida	-		-	-	-	0.9	± 0.9	0.3			± 0.3	-	-	-	-		± 0.2
i ciciioiiiles		Etheostoma exile	0.4	±	0.3	I .	± 2.5	-	-	0.6	± 0.8	0.1	± 0.1	-	-	-	-		± 1.2
		Etheostoma flabellare	-		-	I .	± 0.1	-		-		-		-	-	-	-		± 0.6
		Etheostoma nigrum	0.1	±	0.6	0.5		0.1		0.8		0.2			0.2	2 -			± 1.5
	Percidae	Etheostoma olmstedi Percina caprodes	8.5 1.0	±	19.9 2.9	7.6 : 4.7 :	± 17.2 ± 12.2		± 41.4 ± 33.6	2.3	± 26.9 ± 5.2	8.2 0.9	± 12.5 ± 2.3		9.9		± 9.2 ± 4.6	9.6	± 21.7 ± 12.8
		Percina caproaes Percina copelandi	0.6	±	0.8	- 4.7	- 12.2	- 0.9	± 33.0 -	l .	± 5.2 ± 1.8	0.9		0.9 ±		0.4		0.1	
		Perca flavescens	8.2		15.6	11.4	± 17.9	11.3	± 27.7	l .	± 42.7		± 14.2	19.9 ±			± 3.5	14.2	
		Sander canadensis	-	-	-		± 0.7		± 0.2	0.5		-	-	0.2 ±			± 1.0	0.2	
		Sander vitreus	0.2	±	0.1	0.9			± 1.1	0.4		0.5	± 0.3	0.1 ±			± 0.4	0.2	
	Sciaenidae	Aplodinotus grunniens	-		-	-	-	-	-		± 0.2	-	-	-	-	-	-	0.4	
Percopsiformes	Percopsidae	Percopsis omiscomaycus	0.6	±	0.8	0.2	± 3.0	7.1	± 34.0	9.7		1.0	± 6.9		4.4	2.0	± 4.3	2.7	
		Ichthyomyzon unicuspis	0.6	±	0.8	-	-	-	-	-	-	-	-	-	-	-	-		± 0.3
Scorpaeniformes	Cottidae	Cottus bairdii	0.6	±	0.8	0.3		_	± 0.9	-	- (1.0	-	- 26.7	-	- 1.5	-	-	_	± 0.2
		Ameiurus nebulosus Ictalurus punctatus	0.9	±	0.5	0.4	± 1.4	0.4 0.9	± 1.9 ± 0.9	9.0		5.2	± 26.7 ± 0.8	0.2 ±	1.5	-	-	0.3	± 26.5 ± 0.5
Siluriformes	Ichtaluridae	Noturus flavus	_		-		-	0.9	± U.9	U.b :	± 0.8	0.6	± 0.8	0.6 ±	0.7	_	-	0.3	
		Noturus gyrinus	0.6	±	0.8	0.7	± 0.5	]	-	0.7	± 0.3	0.2	± 0.7		0.7	_	-	0.9	
	L	rvotarus gyrinus	0.0	Ţ	0.0	U./ :	<u>.</u> U.5			0.7	<u>.</u> ∪.5	0.2	± U./	U.1 ±	. 0.2	-		0.0	± 0.4

Table S3: Average ( $\bar{x} \pm \text{SD}$ ) abundance of each species sampled by gillnets in the RSI from 1995 to 2012 in each sectors targeted of the St. Lawrence River. A total of 45 species from 20 families were collected. It appears that no sector is home to all species captured at the river scale.

				LSF		ı	LSL		N	/IS	A-	LSP	I	LSP	,		ВВ		SSN	١	To	tal
	Number of sta	tions	198		222		79		1	87	23		238		231		104		12	259		
Ordre	Famillies	Species	x	± S	D	x	± SI	D	x:	± SD		: SD	x	± S	D	x	± SD	x	± S	D		t SD
A -iif	A -ii-l	Acipenser fulvescens	0.4	±	0.2	1.9	±	3.6	1.1	± 1.7		± 1.8	0.8	±	1.7	1.8	± 3.0	2.7	±	4.6	1.3	± 2.7
Acipenseriformes	Acipenseridae	Acipenser oxyrinchus	-		-	-		-	-	-	-	-	-		-	0.4	± 0.7	1.0	±	1.0	0.2	± 0.4
Amiiformes	Amiidae	Amia calva	-		-	0.1	±	0.1	-	-	0.2	± 0.8	0.1	±	0.1	0.1	± 0.1	-		-	0.3	± 0.3
		Alosa pseudoharengus	0.2	±	0.6	0.2	±	1.8	-	-	0.1	± 1.1	0.4	±	2.6	0.4	± 0.7	0.4	±	1.1	0.2	± 1.5
Clupeiformes	Clupeidae	Alosa sapidissima	-		-	0.1	±	0.6	-	-	1.3	± 9.3	0.3	±	1.8	0.5	± 2.4	-		-	0.4	± 3.8
		Dorosoma cepedianum	-		-	-		-	-	-	0.3	± 0.2	-		-	-	-	-		-	0.5	± 0.9
		Catostomus catostomus	-		-	-		-	0.1	± 0.5	0.5	± 0.7		±	0.9	0.1	± 0.5	3.3	±	4.5	0.3	± 1.6
		Catostomus commersonii	1.3	±	1.7	1.9		1.7	0.7	± 1.3	0.7	± 1.3	3.4	±	3.6	1.1	± 2.0	1.7	±	2.1	1.5	± 2.4
	Catostomidae	Carpiodes cyprinus	-		-	0.9	±	0.6	-	-	0.2	± 0.7	-		-	0.9	± 0.1	-		-	0.4	± 0.4
		Moxostoma anisurum	0.6	±	0.3	0.6	±	1.3	0.1	± 0.4	0.2	± 0.7	0.6	±	1.3	0.6	± 1.0	1.0	±	1.0	0.4	± 0.9
Cypriniformes		Moxostoma macrolepidotum	1.0	±	0.6	0.8	±	1.8	0.8	± 1.2	1.5	± 2.4	3.2	±	4.1	3.2		2.2	±	3.3	1.8	± 3.7
Cyprilliornies		Cyprinus carpio	0.2	±	0.2	0.4	±	1.4	0.2	± 0.8	0.6	± 1.0	0.4	±	1.3	2.0	± 3.1	0.2	±	0.1	0.4	± 1.6
		Hybognathus regius	-		-	-		-	-	-	0.5	± 0.6	0.8	±	0.1	-	-	-		-	1.0	± 0.2
	Cyprinidae	Notemigonus crysoleucas	8.0	±	4.4	0.4	±	2.7	0.9	± 0.7	2.4	± 1.4	1.5	±	5.7	2.0	± 13.6	5 -		-	1.3	± 7.8
		Notropis hudsonius	2.0	±	7.8	0.6	±	2.9	0.6	± 0.3	0.1	± 0.5	0.8	±	2.8	0.2	± 2.0	-		-	0.6	± 3.5
		Semotilus corporalis	0.6	±	0.7	-		-	-	-	-	-	-		-	-	-	-		-	0.8	± 0.3
Esociformes	Esocidae	Esox lucius	1.9	±	2.4	1.7	±	3.2	0.6	± 1.6	1.4	± 2.3	2.3	±	3.5	0.8	± 2.2	-		-	1.4	± 2.8
Esocilornies	Lsocidae	Esox masquinongy	0.6	±	0.7	0.5	±	0.2	0.1	± 0.1	-	-	0.4	±	0.6	0.4	± 0.4	-		-	0.2	± 0.2
Gadiformes	Gadidae	Microgadus tomcod	-		-	-		-	-	-	-	-	-		-	-	-	1.0	±	1.0	0.8	± 0.3
Gaulionnes	Lotidae	Lota lota	-		-	-		-	0.3	± 0.2	0.2	± 0.1	0.1	±	0.1	0.2	± 0.1	1.0	±	1.0	0.1	± 0.1
Lepisosteiformes	Lepisosteidae	Lepisosteus osseus	0.3	±	0.2	0.1	±	0.5	-	-	0.5	± 0.7	0.4	±	0.6	-	-	-		-	0.3	± 0.2
Osmeriformes	Osmeridae	Osmerus mordax	-		1	-		7	-	-	0.5	± 0.7	-		-	-	-	-		-	0.8	± 0.3
Osteoglossiformes	Hiodontidae	Hiodon tergisus	-		-	1.3	±	4.9		± 0.4	1.3	± 3.3	1.6	±	3.8	0.4	± 1.3	0.3	±	0.2	0.9	± 3.4
		Ambloplites rupestris	8.4	±	1.4	4.5	±	5.9	1.7	± 2.6	1.0	± 1.5	0.5	±	1.2	0.5	± 0.9	1.0	±	1.0	2.5	± 5.7
		Lepomis gibbosus	0.9	±	1.9	0.7	±	2.9	0.4	± 0.3	0.2	± 0.6	0.3	±	0.7	0.4	± 0.7	-		-	0.4	± 1.3
	Centrarchidae	Lepomis macrochirus	0.6	±	0.7	-		-	-	7-	-	-	-		-	-	-	-		-	8.0	± 0.3
	Centrarchidae	Micropterus dolomieu	1.2	±	2.8	1.8	±	2.7	0.7	± 1.4	0.6	± 1.1			1.0	0.8	± 1.6	0.3	±	0.7	0.9	± 1.9
		Micropterus salmoides	0.5	±	1.5	0.4	±	1.5	-	-	0.2	± 0.9	0.4	±	0.2	0.2	± 0.1	-		-	0.2	± 0.9
		Pomoxis nigromaculatus	0.8	±	0.4	0.2	±	0.1	-		0.2	± 0.8	-		-	0.3	± 0.2	-		-	0.5	± 0.4
Perciformes	Gobiidae	Neogobius melanostomus	0.8	±	0.3	0.2	±	0.3	1	-	0.2	± 0.1	0.8	±	0.3	0.2	± 0.1	-		-	0.3	± 0.2
reichornies	Moronidae	Morone americana	-		-	0.4	±	0.2	0.1	± 0.1	0.3	± 1.7	0.7	±	0.3	0.3	± 1.3	0.2	±	0.5	0.1	± 0.9
	Wioromuae	Morone saxatilis	-		-	-		-	-	-	-	-	-		-	0.1	± 0.1	-		-	0.2	± 0.6
		Percina caprodes	-		-	1.0	±	0.9	-	-	-	± 0.1	0.8	±	0.4		± 0.1	-		-	0.2	± 0.2
	Percidae	Perca flavescens	34.5	±	31.3	43.4	±	65.9	4.4	± 7.0	7.9	± 1.5	17.8	±	24.8	5.8	± 11.9	0.1	±	0.4	18.8	± 36.3
	reicidae	Sander canadensis	-		-	0.8	±	3.0	0.8	± 1.2	1.9	± 2.4	1.7	±	2.7	2.5	± 3.4	5.6	±	6.8	1.7	± 3.7
		Sander vitreus	0.8	±	1.2	5.4	±	6.8	1.5	± 1.5	2.9	± 2.7	4.2	±	3.7	2.9	± 3.3	2.5	±	2.5	3.8	± 4.0
	Sciaenidae	Aplodinotus grunniens	-		-	0.5		0.3	-	-		± 0.3	0.3	±	0.2	0.4	± 0.7	1.0	±	1.0	0.3	± 0.2
Percopsiformes	Percopsidae	Percopsis omiscomaycus	-		-	0.5	±	0.7	-	-	0.2	± 0.1	0.2	±	0.1	0.4	± 0.7	-		-	0.7	± 0.8
Petromyzontiformes	Petromyzontidae	Ichthyomyzon unicuspis	-		-	0.6	±	0.3	0.1	± 0.1	0.3	± 0.2	0.2	±	0.1	0.1	± 0.1	_		1.0		± 0.2
		Coregonus clupeaformis	-		-	-		-	-	-	-	-	0.4	±	0.3	-	-	1.0	±	1.0	8.0	± 0.1
Salmoniformes	Salmonidae	Onchorhynchus kisutch	0.6	±	0.7	-		-	-	-	-	-	-		-	-	-	-		-	8.0	± 0.3
		Oncorhynchus tshawytscha	0.6	±	0.7	-		-	-	-	_	± 0.7	-		-	-	-	-		-	0.2	± 0.4
		Ameiurus nebulosus	0.3	±	0.7	0.3	±	1.0	0.2	± 0.7	2.8	± 6.9	3.2	±	9.7	0.4	± 1.5	-		-	1.2	± 5.3
Siluriformes	Ichtaluridae	Ictalurus punctatus	-		-	0.4	±	0.9	0.5	± 1.3	0.5	± 1.8	1.3	±	2.3	1.3	± 3.9	1.6	±	2.5	0.7	± 2.3
		Noturus flavus	-		-	-		-	-	-	-	-	-		-	0.4	± 0.7	-		-	8.0	± 0.3

Table S4: Indicator species of the overall littoral vs. pelagic communities in the St.

Lawrence River (IndVal analysis; Dufrene & Legendre, 1997).

Significance was tested using a random permutation procedure and the "Holm" adjustment method (Holm, 1979) was used to correct for multiple testing (De Cáceres, Legendre & Moretti, 2010).

Habitats	Species
	Alosa pseudoharengus
	Culaea inconstans
	Cyprinella spiloptera
	Etheostoma exile
	Etheostoma nigrum
	Etheostoma olmstedi
	Fundulus diaphanus
	Hybognathus regius
	Labidesthes sicculus
	Lepomis gibbosus
	Negobius melanostomus
	Notropis atherinoides
T :441	Notropis bifrenatus
Littoral	Notemigonus crysoleucas
	Noturus gyrinus
	Notropis heterodon
	Notropis heterolepis
	Notropis hudsonius
	Notropis rubellus
	Notropis stramineus
	Notropis volucellus
	Osmerus mordax
	Percina caprodes
	Percina copelandi
	Percopsis omiscomaycus
	Pimephales notatus
	Semotilus corporalis
	Acipenser fulvescens
	Aplodinotus grunniens
	Catostomus catostomus
	Esox lucius
D 1 '	Hiodon tergisus
Pelagic	Ictalurus punctatus
	Ichthyomyzon unicuspis
	Lota lota
	Sander canadensis
	Sander vitreus

Table S5: Average dissimilarity (Bray-Curtis, log-transformed abundance) among sectors for littoral (a) and pelagic (b) fish communities.

a)

SECTORS	Lake Saint- François (LSF)	Lake Saint- Louis (LSL)		Archipelago of Lake Saint- Pierre (A-LSP)	Lake Saint- Pierre (LSP)	Bécancour- Batiscan (BB)
Lake Saint-Louis (LSL)	33.16					
Montréal-Sorel (MS)	47.26	43.55				
Archipelago of Lake Saint-Pierre (A-LSP)	47.80	40.18	39.98			
Lake Saint-Pierre (LSP)	49.14	44.72	50.21	44.35		
Bécancour-Batiscan (BB)	48.04	42.28	40.82	40.24	46.86	
Grondines-Saint-Nicolas (GSN)	70.52	66.54	56.12	62.01	63.36	52.08

b)

SECTORS	Lake Saint- François (LSF)	Lake Saint- Louis (LSL)		Archipelago of Lake Saint- Pierre (A-LSP)	Lake Saint- Pierre (LSP)	Bécancour- Batiscan (BB)
Lake Saint-Louis (LSL)	35.38					
Montréal-Sorel (MS)	56.52	54.69				
Archipelago of Lake Saint-Pierre (A-LSP)	51.95	38.97	55.48			
Lake Saint-Pierre (LSP)	44.87	30.74	57.56	36.98		
Bécancour-Batiscan (BB)	54.28	34.96	53.57	38.53	29.66	
Grondines-Saint-Nicolas (GSN)	74.21	61.02	57.72	58.65	55.94	49.61