

Spatial organisation of fish communities in the St. Lawrence River: a test for longitudinal gradients and spatial heterogeneities in a large river system

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Abstract Typified by heterogeneous habitats, large rivers host diversified communities throughout their course. As the spatial organisation of fish communities within these ecosystems remains little studied, longitudinal gradients and spatial heterogeneities of fish diversity were analysed in the large temperate St. Lawrence River, Canada. We used two distinct datasets obtained from either seine nets or gillnets from governmental standardised fish surveys (1995–2012) consisting of a total of

299,662 individuals from 76 fish species captured in 1,051 sites. Results from diversity indices and multi-variate analysis revealed a gradual downstream increase in taxonomic diversity, and a gradual change of the community structure along the river. In addition, we observed different fish communities within fluvial lakes and corridors and found significant differences in fish community structure between opposite shores. The fish communities described along the river using seine nets are spatially more heterogeneous than when described using gillnets. This discrepancy is likely resulting both from the more mobile species targeted by gillnets and sampling sites located farther from the shallower shoreline habitat targeted by seine nets. The organisation of fish communities stresses the need to implement science-based policies and actions to preserve biodiversity and restore communities distributed over large heterogeneous ecosystems.

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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 recognised as primary forces shaping the spatial distribution of fish communities (Robinson et al., 2002; Ward et al., 2002; Nilsson et al., 2005). Albeit widely studied in streams and small- to medium-sized rivers (Pekárik et al., 2011; Suvarnaraksha et al., 2012; Konan et al., 2015), only a few large rivers were studied over extensive stretch (e.g. Missouri: Galat et al., 2005; Ganges: Das et al., 2013; Mekong: Chea et al., 2016) 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 $7,500 \text{ m}^3 \cdot \text{s}^{-1}$ and their watershed is larger than $900,000 \text{ km}^2$ (Bethemont, 2003).

In past years, several theoretical concepts focusing on communities organisation along entire river systems were proposed (reviewed in Johnson & Host, 2010; Melles et al., 2012; Ellis & Jones, 2013). For example, the River Continuum Concept (RCC; Vannote et al., 1980) describes rivers as a longitudinal gradient of environmental conditions shaping the distribution and organisation of communities from the headwater to the river mouth (e.g. Naiman et al., 1987; Jiang et al., 2011; Wolff et al., 2013). In parallel, the Serial Discontinuity Concept (SDC; Ward & Stanford, 1983, 1995) predicts that natural and anthropogenic disruptions will lead to longitudinal discontinuities in biological organisation at the population (e.g. abundance), community (e.g. richness, dominance) or even at the ecosystem levels (e.g. productivity). The SDC is a conceptual framework often used to explain the effects of dams, tributaries or geomorphological discontinuities on biological organisation in the river continuum (Hillbricht-Ilkowska, 1999; Stanford & Ward, 2001; Kiffney et al., 2006).

Considering the river as a single flowing channel, both RCC and SDC do not offer a complete perspective on the spatial heterogeneity of fish organisation in

large river systems (e.g. Sedell et al., 1989; Johnson et al., 1995; Dettmers et al., 2001; Araújo et al., 2009). On the other hand, integrative theoretical concepts with a broader framework were developed (e.g. Riverscape and River Wave Concepts, Poole, 2002; Humphries et al., 2014). For example, the concept of riverscape (Fausch et al., 2002; Poole, 2002; Wiens, 2002), which recognised the importance of continuous, hierarchical and heterogeneous properties of rivers, integrates longitudinal gradients and discontinuities within a spatially explicit framework (e.g. Massicotte et al., 2014; Le Pichon et al., 2017). This concept assumes that while geomorphologically distinct entities (e.g. fluvial lakes, rapids, channelized areas, etc.) observed along a riverscape (i.e. between 1 and 100 km; Fausch et al., 2002) are ecologically connected along the upstream–downstream axis, they nevertheless possess unique biological characteristics owing to local spatial heterogeneity (importance of uniqueness, Poole, 2002). Considering the overall heterogeneity of the river at different spatial scales, the riverscape concept may ultimately help explaining the complex biotic community patterns observed in large rivers (e.g. Frenette et al., 2012; Massicotte et al., 2014; Gladyshev et al., 2015).

The main objective of this study was to assess the spatial organisation of fish communities in a large temperate river across multiple spatial scales. Specifically, we (1) characterised fish diversity along the longitudinal upstream–downstream axis of the St. Lawrence River (Québec, Canada), (2) identified potential longitudinal discontinuities along north and south shores and (3) assessed relationships between riverscape heterogeneity and fish communities at (i) hydro-morphological (fluvial lakes vs. corridors), (ii) sector and (iii) shore scales. To fulfil these objectives, we analysed the fish community structure using a large dataset covering the St. Lawrence River from Cornwall to Québec City (424 km stretch). The portion studied is highly heterogeneous both longitudinally and transversally (i.e. between opposing shores) due to the hydro-morphological characteristics of water bodies. We predicted that species distribution along the St. Lawrence River is associated with the longitudinal series of fluvial lakes alternating with narrow corridors, rapids, archipelagos, and the presence of a freshwater tidal zone in the downstream portion. Moreover, as the deep navigational channel is dividing the river in a northern and southern portion

along its course, we expected that fish communities are structured differently along each shore.

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 et Bouchard 2000). The St. Lawrence River drains the North American Great Lakes, which contains more than 20% of all freshwater reserves of the world, to the Gulf of St. Lawrence which is connected to the Atlantic Ocean.

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 ≥ 300 m; depth ≥ 11.3 m downstream Montréal harbour and ≥ 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. Indeed, three main water masses are flowing side-by-side without mixing in the portion upstream of Trois-Rivières (Frenette et al., 2006; Hudon & Carignan, 2008). Downstream of this area, mixing occurs as the influence of tides increases and even tidal flow reversal is noticeable downstream of Donnacona

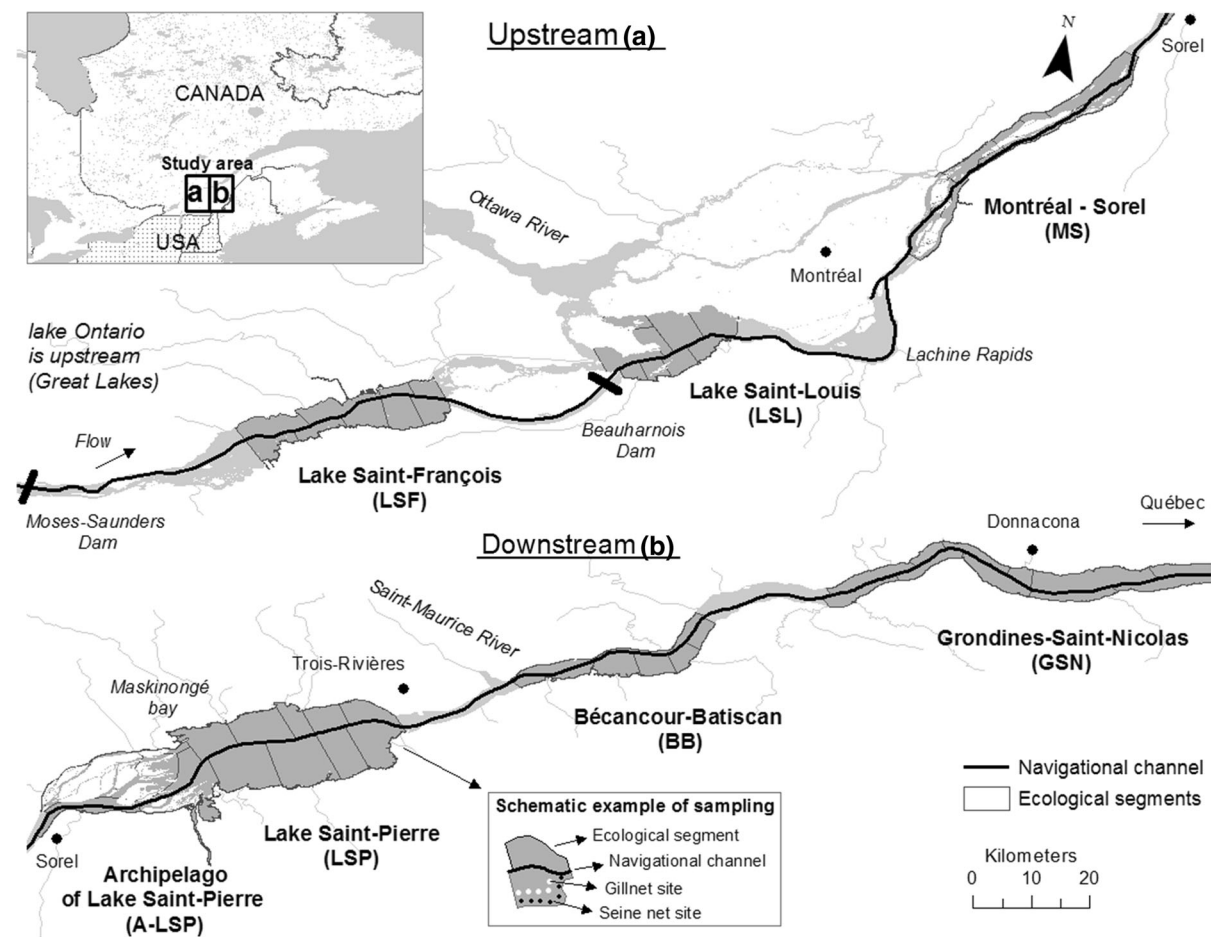


Fig. 1 Map of the sectors studied (1-LSF, 2-LSL, 3-MS, 4-A-LSP, 5-LSP, 6-BB and 7-GSN) along the St. Lawrence River. The ecological segments and the navigation channel separating

the shores are also shown. Note that for clarity the map was cut into two portions (upstream, upper part and downstream, lower part)

(Fig. 1, Centre-Saint-Laurent, 1998). 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 stabilised and its 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 (Ministère de la Faune, des Forêts et des Parcs du Québec data bases). Fish richness in the St. Lawrence River is relatively high and comparable to Mississippi River (102 species), while it is more diversified than Volga (63 species) or Danube (58 species; Galat & Zweimüller, 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 standardised fish survey

The standardised governmental fish survey in the St. Lawrence River, known as the RSI (“Réseau de Suivi Ichtyologique”, described in La Violette et al., 2003), characterises the fish community structure at the end of the growing season (August to October). Due to such late sampling, and the sampling gear employed, only relatively large juvenile (> 50 mm) to adult were captured. The whole river is divided in seven different areas (hereafter called sectors) according to their specific hydrological and morphometric characteristics. We thus recognise (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). Numbers were added to sector acronyms to ease locate them along the upstream/downstream axis of the river (Fig. 1). The fluvial lakes observed along the St. Lawrence River are natural (e.g. not man-made). Although seemingly analogous to pools observed along a stream gradient, they are functionally dissimilar since fluvial lakes are not associated with the presence of deeper portions of the river (i.e. pools) but rather created by water flowing over shallower areas combined with an enlargement of the main tributary. Although Lake Saint-François increased in size after damming the river, it did exist prior to the construction of the Beauharnois Dam. While the last two corridor sectors are contiguous (6-BB and 7-GSN), 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, were not considered in the present study because the powerful hydrodynamic flow regime prevents the use of the standardised sampling surveys protocol.

Fish communities were sampled approximately every one km of shoreline; such sampling scheme was determined as a trade-off between sampling effort versus area covered while allowing enough statistical power to detect significant spatial changes in the community structure (Flotemersch et al., 2011). A multiple-gear approach was implemented in the RSI as it is considered the most efficient approach to assess fish community organisation in large heterogeneous rivers (Galat et al., 2005; De Leeuw et al., 2007). The RSI uses (1) a standardised beach seine net (12.5 m long \times 4 m deep and 3.2 mm stretched mesh) and (2) an array of two multimesh gillnets (60 m long \times 1.8 m deep; eight panels of 25, 38, 51, 64, 76, 102, 127 and 152 mm stretched mesh, 15–28.5 h fishing period; La Violette et al., 2003). Seine nets were preferred for sampling the fish community in lentic and nearshore littoral habitats (depth < 1.5 m), while gillnets were used for sampling lentic and lotic midshore littoral habitats in the deeper water column adjacent to the seine (depth between 1.5 and 14 m; average of 6.2 m; Fig. 1). Two distinct gears were analysed separately to take into account bias related to selectivity and the specific habitats sampled. Gillnets captured larger and more mobile fishes in a deeper water column located farther from the shallower shoreline habitat targeted by seine nets (La Violette

et al., 2003). Both 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 et al., 2006).

Due to the sheer size of the St. Lawrence River, only one or two sectors were sampled yearly. From 1995 to 2012, all sectors were sampled three times, except for 3-MS, 7-GSN and 6-BB that were sampled one, two and four times, respectively. As we intend to focus on spatial patterns in the present study, we analysed the interaction between the space and time factors to ensure that sites sampled from different years can be pooled into their sectors/segments (defined below). The space–time interaction method (STI) allows testing space–time interaction in repeated ecological survey data, when there is no replication at the level of individual sampling sites (Legendre et al., 2010). A significant interaction would indicate that the spatial structure of the communities has changed between surveys, so that survey results could not be pooled. Due to the RSI sampling design, STI was performed on the five sectors that have been sampled tree times (1-LSF, 2-LSL, 4-A-LSP, 5-LSP, 6-BB) at the sector and segment scales, for both the seine net and gillnet gears. None of the analysis showed significant space–time interaction (Online Resource 1). Since the spatial structure of the fish communities did not change significantly between the RSI sampling periods for both gears, we pooled the site samples from different years into their sectors/segments to better represent the “average” local community structure.

When considering both gears, a total of 1,051 sites were sampled one to four times over the 17-year period (total of 2,386 samples; Online Resource 2). 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. While considering seine net and gillnet samples separately, 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 defined by the general shoreline morphology (i.e. based on 25 specific shapes such as straight,

sinuous, indented, “closed” or “open” bay) observed by satellite imagery and aerial photography (see Fig. 1), and various geomorphologic features describing the physical landscape both below and above water (e.g. sandy vs. rocky shores, presence of cliffs, water velocity, urbanisation, occupation of the coastline, extent of floodplain/intertidal zone, etc.; see DesGranges & Ducruc, 1998). Finally, as the deep navigational channel is dividing the river in a northern and southern portions along its entire course, it was possible to analyse each shore separately for either seine net and gillnet 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 net 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; Online Resource 2).

Indices of diversity

Fish diversity was analysed using three complementary and robust indices. Firstly, the rarefaction index (ES_n) 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 seine net (ES_{70}) and 30 individuals for the gillnet (ES_{30}). 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 sampled using gillnet located in the Montréal–Sorel sector. Secondly, we calculated the Simpson diversity ($1 - \lambda'$) that takes into account both species richness and abundance distribution. Thirdly, we used the average taxonomic distinctness (Δ^* , 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 analysis

All analyses targeting fish communities sampled by either seine net or gillnet were always analysed separately. The smallest statistical unit is represented by the ecological segments rather than sampling sites

(i.e. unit of analyses); all samples collected within an individual ecological segment were pooled without regard to the sampling year. We used a hierarchical subset design to test differences among (i) opposing shores within sectors (north vs. south shores), (ii) sectors (1-LSF, 2-LSL, 3-MS, 4-A-LSP, 5-LSP, 6-BB, 7-GSN) and (iii) hydro-morphological scales (fluvial lakes vs. corridors vs. archipelago).

Longitudinal gradients

Differences in diversity indices among the fixed factors of sectors were tested, one at a time, using a non-parametric permutational multivariate analysis of variance (PERMANOVA, with 9999 permutations; Anderson et al., 2008) with Euclidian distance matrix. PERMANOVA generates the null distribution of the test statistic without assumptions of normality (Fairclough et al., 2008). Moreover, the gradual downstream which increased in diversity indices (i.e. rarefaction index, Simpson diversity and average taxonomic distinctness) was tested using the non-parametric Spearman correlation coefficient (Zar, 1972). As we believe that 7-GSN specificities (e.g. beginning of mesotidal portion of the fluvial estuary) may impede detecting such diversity patterns, Spearman correlations were also performed excluding this most downstream sector.

A multivariate seriation test (Index of Multivariate Seriation: IMS; RELATE procedure with maximum 999 permutations with Bray–Curtis dissimilarity, segments oriented upstream–downstream were compared for each shore separately) was used to determine if fish community structure changes gradually along the longitudinal axis of the river (Somerfield et al., 2002; Clarke et al., 2014). Abundance data were log transformed to adjust the balance between the contributions of dominant and rarer species (Clarke, 1993), and were separately analysed along the north and south shores. If community changes along the St. Lawrence River conform to a stepping-stone model of variation (e.g. segment one is more similar to its neighbouring segments than distant segments while the amplitude of dissimilarity is correlated with distance), the correlation will be maximised and the index, IMS (Rho), would equal the highest value (= 1). IMS results were visualised using non-metric multi-dimensional scaling plot (nMDS plot).

Longitudinal discontinuities

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 et al., 2011). A Multivariate Regression Tree (MRT) was used to identify discontinuities along the upstream–downstream gradient of north and south shores of St. Lawrence River using log-transformed species abundance (segments oriented upstream–downstream were compared for each shore separately). The result is a tree whose “leaves” (terminal groups of segments) are made up of subsets of segments, which minimise the within-group sums of squares.

Spatial heterogeneities

Differences among fish community structure (log-transformed abundance, Bray–Curtis dissimilarity) among the fixed factors of (i) opposing shores within sectors (north vs. south), (ii) sectors and (iii) hydro-morphological units (fluvial lakes vs. corridors vs. archipelago) were investigated using PERMANOVA with 9999 permutations. Due to small number of permutations for all treatments when comparing shores within sector, Monte Carlo *P* values (pmc) were used (Anderson et al., 2008).

Community structure discriminated according to the abovementioned factors was compared using a Principal Coordinate Analysis (PCoA; Anderson et al., 2008) that represents the distance between every pair of segments in a two-dimensional array (only axis 1 and 2 were considered). The PCoA was combined to an Indicator Species Analysis (IndVal; Dufrene & Legendre, 1997) that identify species significantly associated to the various fixed factors considered (e.g. considering only the north shore sampled using seine net, what are the species significantly associated to 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 (4-A-LSP) requires the IndVal to be coupled to a multi-levels pattern analysis (e.g. De Cáceres et al., 2010; Casatti et al., 2012). Significance was tested using a random permutation procedure (Dufrene & Legendre, 1997). IndVal analysis was also performed to identify indicator species in each seven sectors (1-LSF, 2-LSL,

3-MS, 4-A-LSP, 5-LSP, 6-BB, 7-GSN), in each hydro-morphological units and to contrast the fish community sampled by seine net and gillnet at river scale.

All analysis were performed using PRIMER-PERMANOVA (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 analysis and *multipatt* function for the IndVal analysis. A significant level of $\alpha = 0.05$ was used for all statistical tests. The “Holm” adjustment method (Holm, 1979) was used to correct the significance level when multiple comparisons were done (with *p.adjust* function in R, De Cáceres et al., 2010).

Results

Fish communities collected

The entire dataset encompassed a total of 299,662 individual fish belonging to 76 species and 25 families (Online Resource 3). A total of 249,309 fish were captured by seine nets in nearshore littoral habitats (< 1.5 m), while 50,353 fish were captured by gillnets in midshore littoral habitats (> 1.5 m). The two gears captured different array of species in all sectors of the St. Lawrence River (PERMANOVA, $P < 0.001$); the seine net collected 71 species belonging to 24 families while the gillnet captured 45 species belonging to 20 families. The number of species observed per sample varied from 0 to 26 species (mean \pm SD: 8.3 ± 4.6) for seine net sites and 0 to 18 species (6.4 ± 2.8) for gillnet sites. As revealed by the IndVal analyses, the community captured by seine net was composed of 27 indicator species, including several Cyprinids, whereas ten species, including larger and more mobile fishes, such as *Acipenser fulvescens* and *Lota lota*, characterised the community captured by gillnet (Online Resource 4).

Longitudinal gradients

Diversity indices

From upstream to downstream, the total number of species changed from 46 species in 1-LSF, 58 in 2-LSL, 52 in 3-MS, 55 in 4-A-LSP, 56 in 5-LSP, 56 in 6-BB and finally 37 in 7-GSN. In 1-LSF, all diversity

indices for both seine net and gillnet were low (Fig. 2). Conversely, except for the average taxonomic distinctness for community collected by seine net (Fig. 2e), the 4-A-LSP exhibited high values of diversity. Illustrating the complementarity of information brought by the various indices, despite the fact that 7-GSN showed high average taxonomic distinctness values for both gears (Fig. 2e, f), 7-GSN had lower values for rarefaction indices (i.e. expected richness for ES_{70} and ES_{30} , see “Methods”) and Simpson diversities ($1 - \lambda'$). The 2-LSL community captured by seine net exhibited high values of rarefaction and Simpson indices (Fig. 2a, c) but not the community captured by gillnet (Fig. 2b, d). For both gears, 6-BB exhibited high values of three diversity indices while 5-LSP and 3-MS showed intermediate values. Only the average taxonomic distinctness values in successive sectors gradually increase from the headwater to the river mouth for the communities captured by seine net (Spearman correlation coefficient of 0.86, $P = 0.01$, Fig. 2e). However, when excluding 7-GSN that marks the beginning of mesotidal portion of the fluvial estuary, the rarefaction index (Spearman correlation coefficient of 0.94, $P = 0.008$), the Simpson diversity (Spearman correlation coefficient of 0.83, $P = 0.02$), and the average taxonomic distinctness (Spearman correlation coefficient of 0.77, $P = 0.05$) also gradually increase downstream for communities captured by gillnet (Fig. 2b, d, f). Conversely, even when 7-GSN was excluded, the rarefaction index and Simpson diversity for communities captured by seine net still do not support a significant downstream increase (Fig. 2a, c).

IMS results

Results from the Index of Multivariate Seriation (IMS) analysis revealed that fish communities gradually changed along the St. Lawrence River with a significant IMS trend ($P < 0.007$; Fig. 3). Rho values indicating the strength of a gradual change along the upstream–downstream axis, were higher for gillnet (0.59) than for seine net (0.48) and higher for north shore (0.64 for both seine net and gillnet) than for south shore communities (0.43 for seine net and 0.56 for gillnet).

Longitudinal discontinuities

The Multivariate Regression Trees (MRT; Figs. 4, 5) highlighted the elevated disparities between sectors

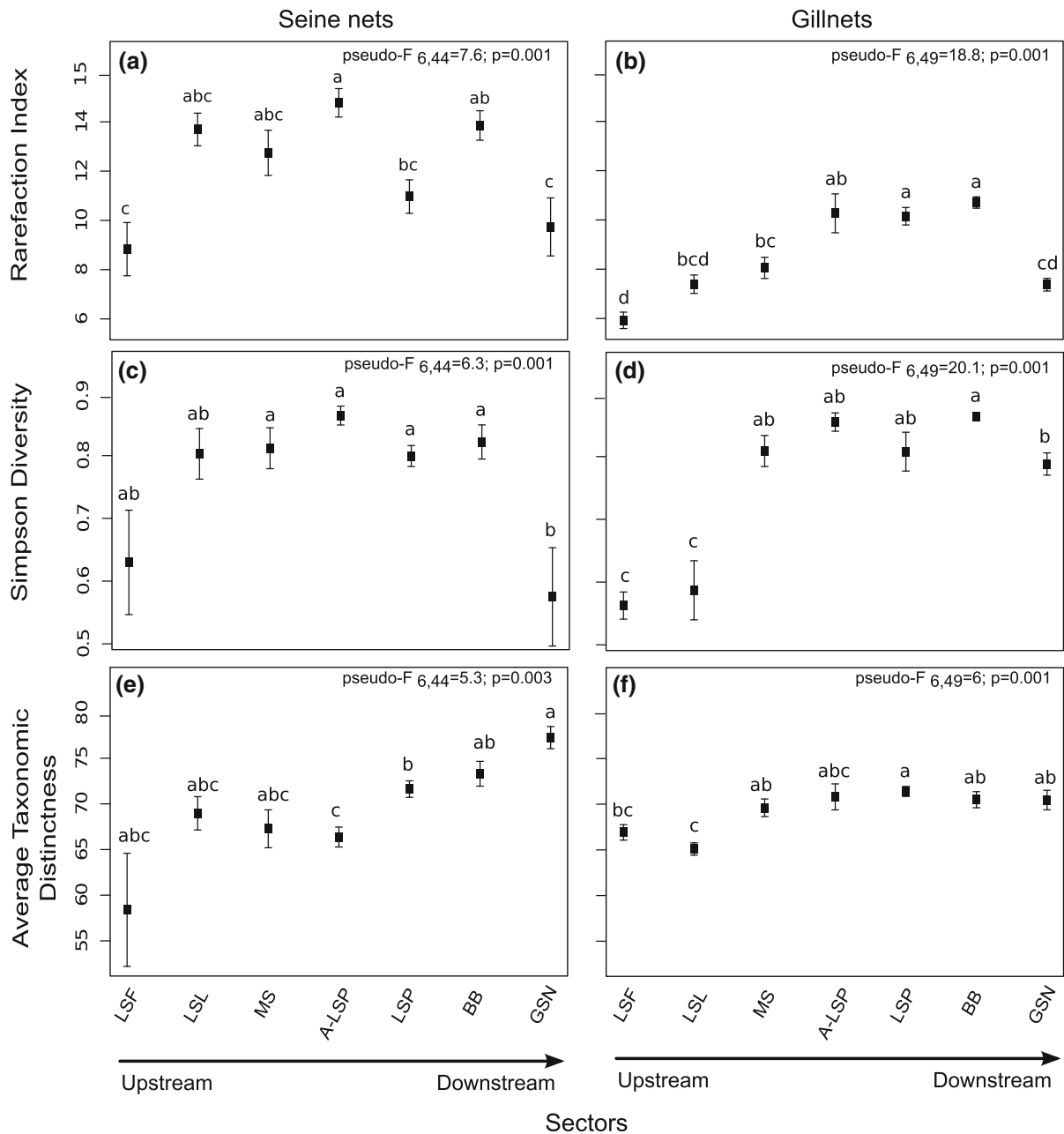


Fig. 2 Point bars showing average values (\pm SE) of rarefaction index (ES_{30} and ES_{70} for gillnets and seine nets, respectively, see “Methods”), Simpson diversity and average taxonomic distinctness among sectors of the St. Lawrence River for fish

communities collected by seine nets (graphs **a**, **c**, **e**) and gillnets (graphs **b**, **d**, **f**). Sectors were ordered from upstream (left) to downstream (right). Different letters above bars represent significant differences ($P < 0.05$)

along the river, such as between the 1-LSF and the 2-LSL separated by a dam. Furthermore, the precision of the MRT analysis even suggest that the St. Lawrence River may be subdivided differently depending on the gear considered compared to the

actual generalisation of the dichotomous lake versus corridor sectors (Fig. 4). For example, the MRT identify a major break in the community captured by seine net of northern 5-LSP (Fig. 4) while such break is inexistent for the community captured by gillnet

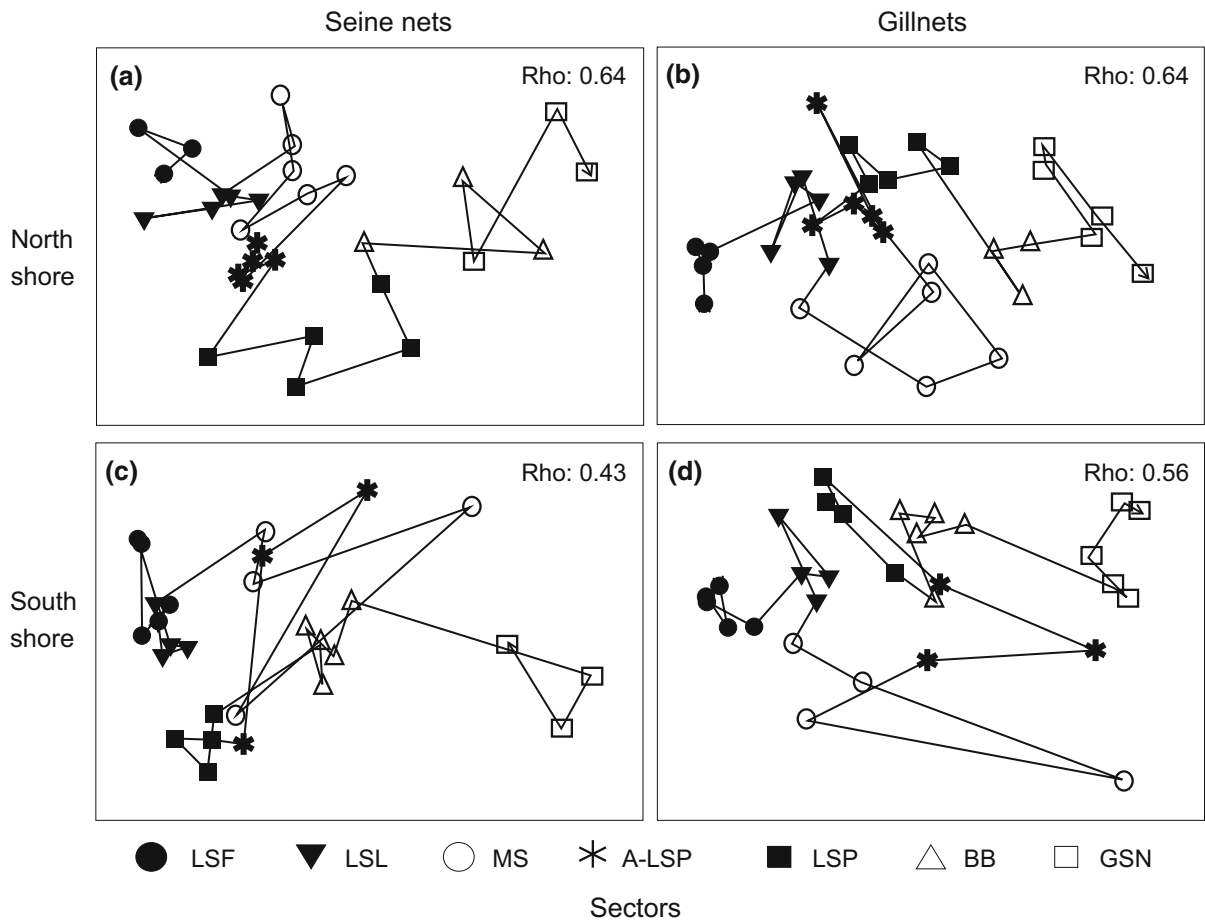


Fig. 3 Index of Multivariate Seriation (IMS) was visualised on a non-metric multidimensional scaling plot representing sequential changes in segments of each sector for seine nets (a, c) and gillnets (b, d) along the north and south shores of the St. Lawrence River. The lines indicate successive segments

along the river (upstream to downstream) where fish communities' changes are significant in all cases ($P \leq 0.007$) and follow a longitudinal gradient. Reading across rows, stress values = 0.15, 0.12, 0.14, 0.09

(Fig. 5). On the other hand, different sectors appeared undifferentiated for some community such as the northern community of the 5-LSP captured by seine net that stretches downstream into the 6-BB sector (Fig. 4).

Spatial heterogeneities

Differences between hydro-morphological units

Fluvial lakes (1-LSF, 2-LSL and 5-LSP), corridors (3-MS, 6-BB and 7-GSN) and the archipelago (4-A-LSP) are home to different fish communities. There were significant differences between hydro-morphological units for the community structure sampled using either

seine net (PERMANOVA; Pseudo- $F_{2,55} = 8.2$; all $P < 0.004$) or gillnet (Pseudo- $F_{2,60} = 10.6$; all $P < 0.02$). These differences were also identified in the PCoA ordination plots (Fig. 6).

In fluvial lakes, four indicator species were identified using IndVal analysis for the community captured by seine net (e.g. *Ameiurus nebulosus* and *Notemigonus crysoleucas*) and seven for the community captured by gillnet (e.g. *Perca flavescens* and *Lepomis gibbosus*). In corridors, four species were also indicators of the seine net (e.g. *Alosa sapidissima* and *Percopsis omiscomaycus*) while none were found for gillnet (Fig. 6). In the archipelago, 11 and nine indicator species were identified for the seine net and the gillnet, respectively. The smaller number of

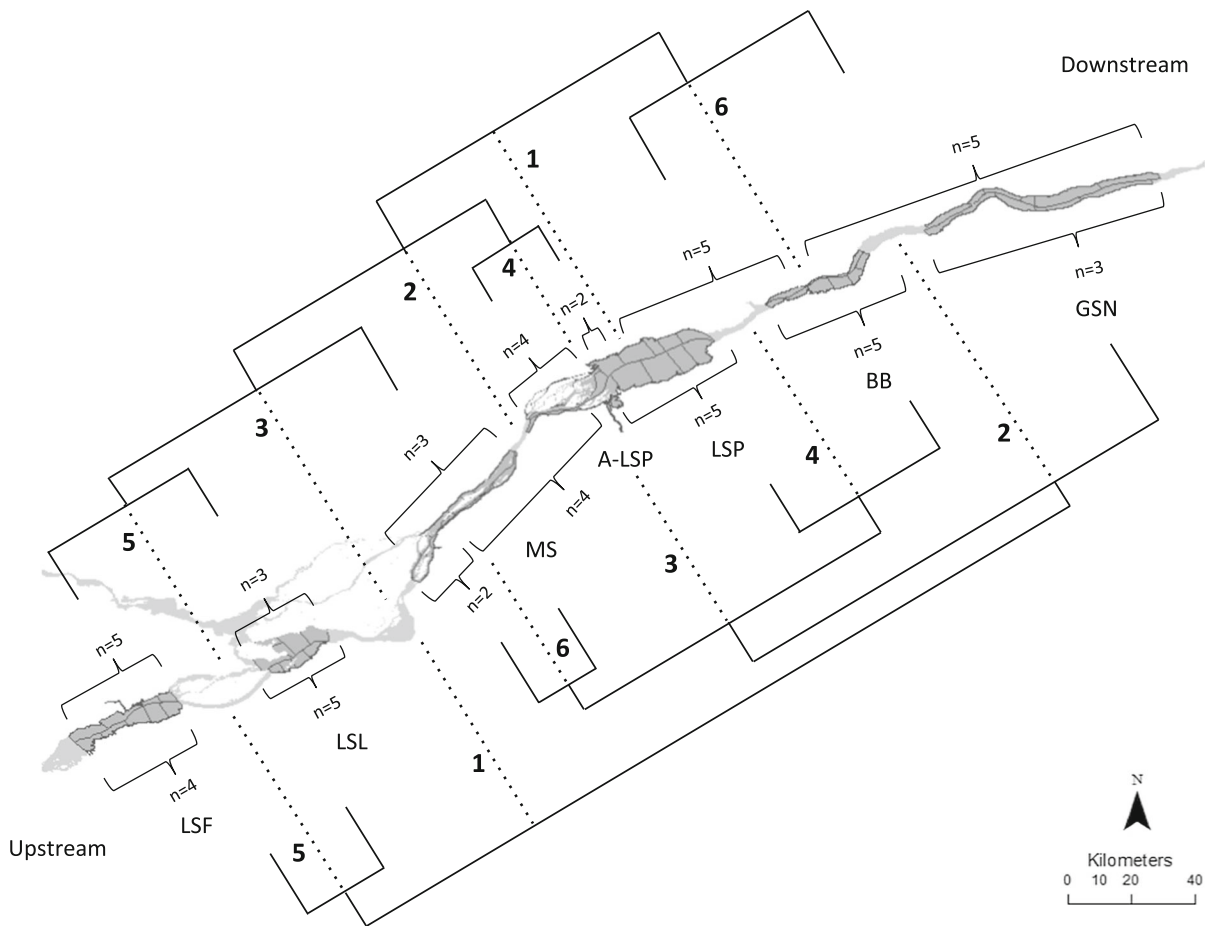


Fig. 4 Discontinuities (dotted line) in fish communities captured by seine nets (with their node numbers) identified along the St. Lawrence River using a Multivariate Regression Tree analysis (MRT). The navigation channel is used to separate the

north from the south shore. For each leaf, the number of segments pooled is indicated. The tree explained 66% and 61.8% of the total sum of squares for the north and south shores, respectively

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 gears, corridor segments are structurally more variable than fluvial lake segments (Fig. 7). This observation is supported by both (1) the non-overlapping confidence intervals between fluvial lakes and corridors and (2) the higher total variance of Bray–Curtis distances observed for the corridor segments (Fig. 7). The variability observed within the archipelago is difficult to judge, as only a few segments were available to calculate Bray–Curtis distances.

Differences among sectors

For both gears analysed separately, almost every sector hosted significantly distinct fish communities (PERMANOVA, all pairwise $P < 0.05$), the only pairwise comparisons not significant were all from the gillnets database (4-A-LSP vs. 2-LSL, 4-A-LSP vs. 5-LSP, 4-A-LSP vs. 6-BB where $P = 0.06$, $P = 0.06$ and $P = 0.1$, respectively), while 7-GSN appears as the most divergent sector (Online Resource 5). This latter result reinforces the observation that the St. Lawrence River is highly heterogeneous at the sector scale.

Some species are indicators of only one sector such as *Notropis stramineus* in 1-LSF and *Apeltes quadracus* in 6-BB for communities captured by seine

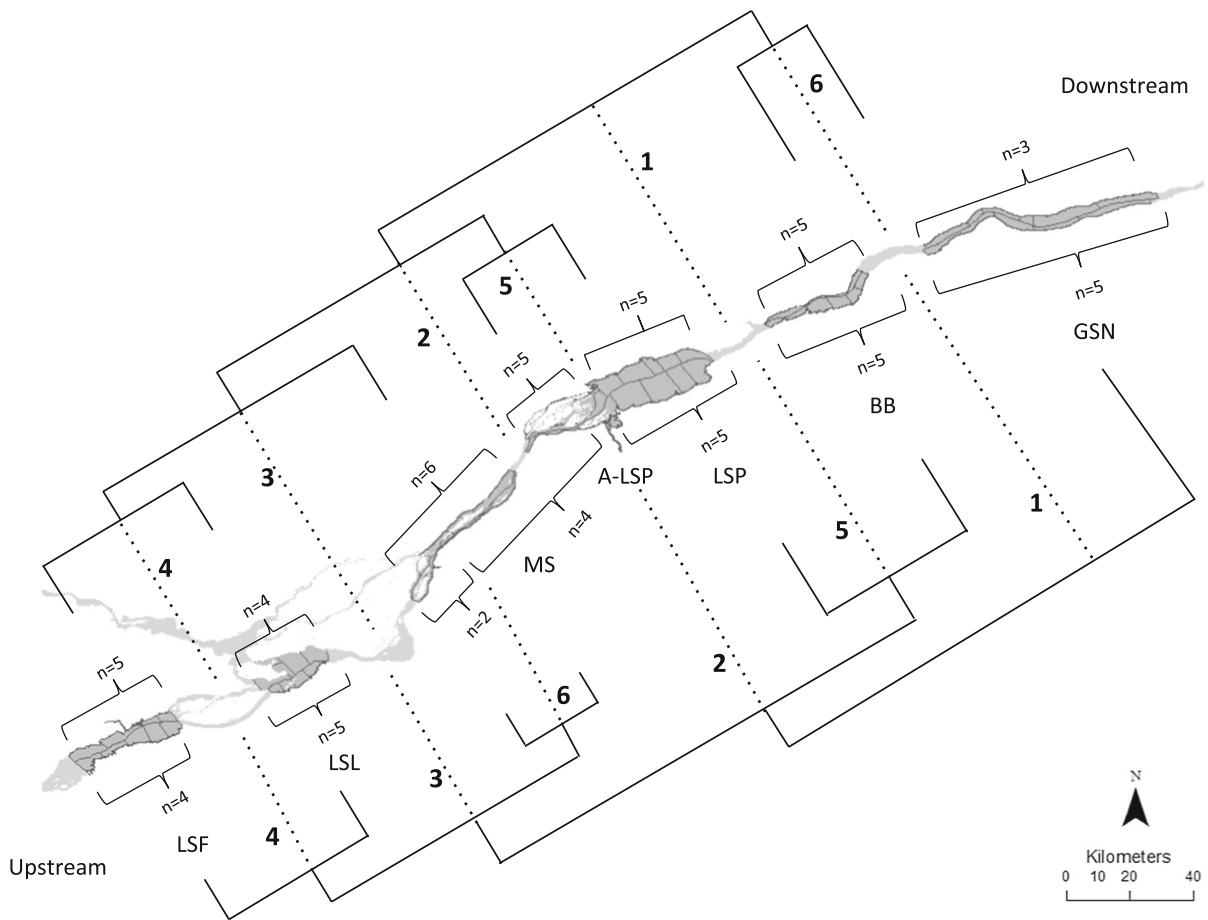


Fig. 5 Discontinuities in fish communities captured by gillnets identified using a Multivariate Regression Tree analysis (MRT): see legend of Fig. 4. The tree explained 70.4% and 76.2% of the total sum of squares for the north and south shores, respectively

net (see complete results in Online Resource 4). In contrast, some species were more common across all sectors with one exception. For example, *Lepomis gibbosus*, *Notemigonus crysoleucas* and *Perca flavescens* were common in all sectors except in 7-GSN for communities captured by seine net (Online Resource 4). Although marine/estuarine species such as *Microgadus tomcod*, *Acipenser oxyrinchus* and *Morone saxatilis* were observed in the 7-GSN sector (Online Resource 3) and contribute to boost the average taxonomic distinctness index, they were not recognised as significant indicator species when using the IndVal analysis.

Differences between shores

The structure of fish communities was significantly different between north and south shores in 2-LSL,

5-LSP and 6-BB sectors for the communities collected by seine net and in 4-A-LSP, 5-LSP and 6-BB for gillnet (PERMANOVA, all $P_{mc} < 0.05$).

Different indicator species were identified in north and south shores. For example, in community captured by seine net, *Cyprinella spiloptera* was identified as an indicator species along the north shore, whereas *Notropis rubellus* was identified along the south shore of the 2-LSL (see complete results in Online Resource 4).

Discussion

The spatial organisation of St. Lawrence fish communities reflects the influence of the river heterogeneity on ecological processes at different spatial scales. It appeared that despite longitudinal gradients, a more

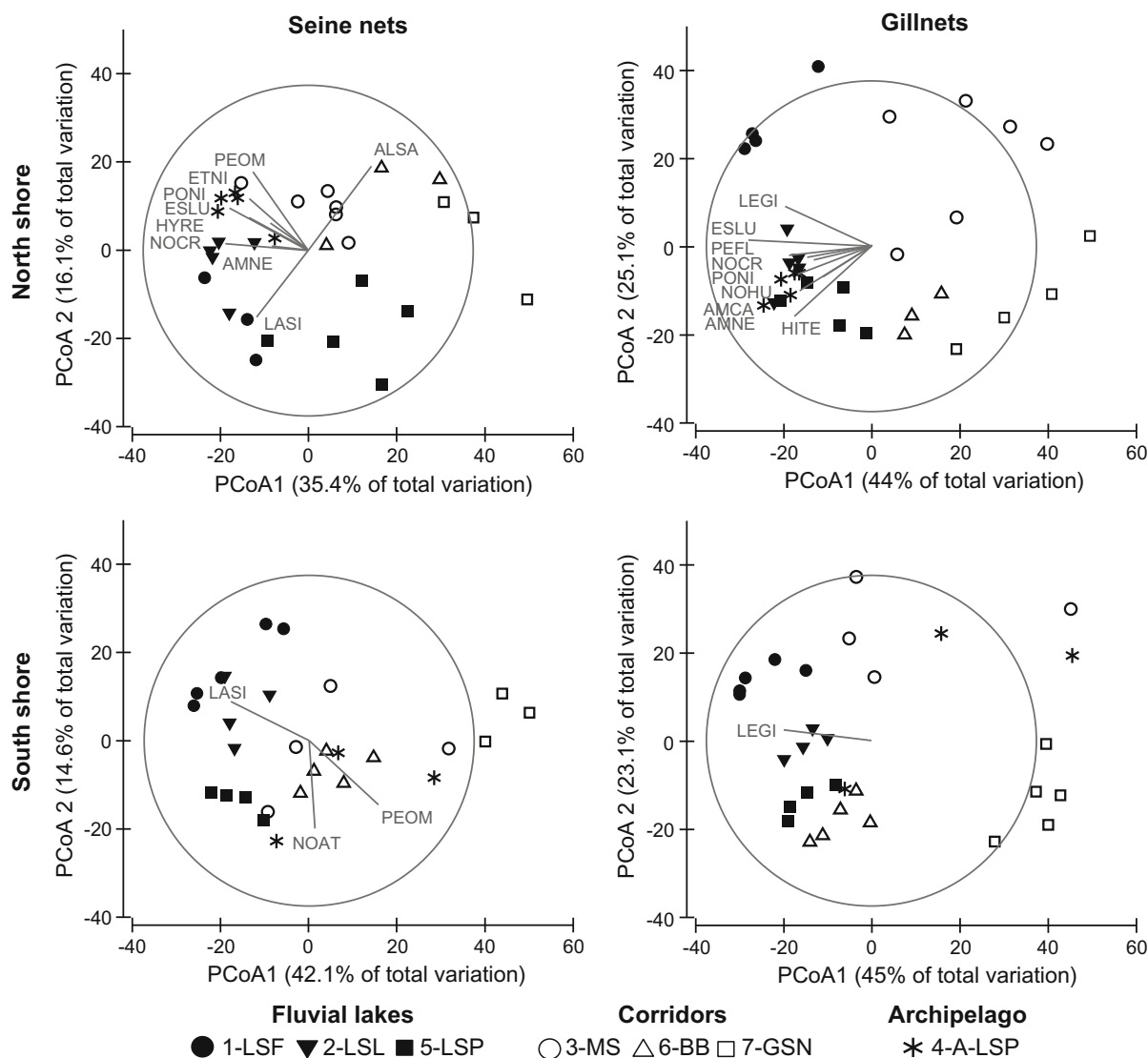


Fig. 6 Principal Coordinate Analysis (PCoA) plots showing fish communities captured by seine nets (**a, c**) and gillnets (**b, d**) at the segment scale among sectors and shores. Indicator species abbreviations, that characterise fluvial lakes (black symbols), corridors (white symbols) and the archipelago (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 PCoA axis 1 and 2, respectively. The length and direction of each vector indicate the strength and sign, respectively, of the relationship between indicator species and the PCoA axes

complex and patchy patterns are defining the spatial organisation of the St. Lawrence River fish communities. The combination of complementary univariate and multivariate analysis 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 gears used and sampling effort (Gotelli &

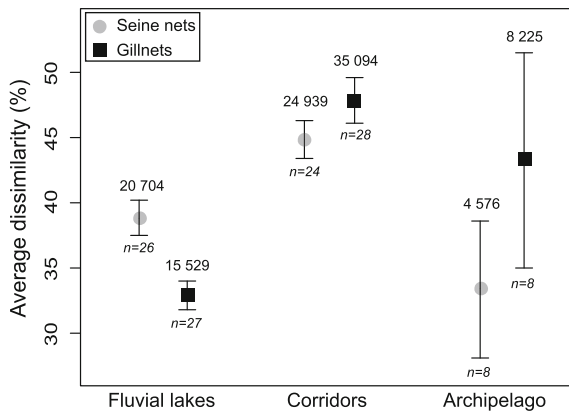


Fig. 7 Point bars showing average values (\pm CI 95%) of Bray–Curtis dissimilarity between the seine nets and gillnets for the fluvial lakes, the corridors and the archipelago of the St. Lawrence River. Numbers on the top correspond to the total variance of Bray–Curtis distances and numbers under the bar correspond to the total number of segments

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. Moreover, the sensitivity of the various univariate diversity indices (e.g. specific vs. taxonomic indices) had to be considered toward their relevance in covering general assembly rules such as ecological gradients.

Longitudinal patterns

The results revealed the presence of a longitudinal component (*i.e.* upstream–downstream axis) of fish communities organisation along the St. Lawrence River; diversified sectors are not only the result of their intrinsic properties but also the result of their geographical position along the continuum. More generally, the longitudinal pattern along the St. Lawrence River appears as a combination of (1) the decreasing anthropogenic habitat alterations from the headwater toward the river mouth and (2) the river-scape heterogeneity along the continuum (e.g. hydro-morphological changes), which increase the dissimilarity between upstream and downstream fish communities and contribute to the gradual increase in taxonomic diversity. Firstly, as predicted by the Serial Discontinuity Concept, the reduced specific and taxonomic fish diversity in the upstream Lake Saint-François (1-LSF) and the distinct communities observed in the adjacent sector of Lake Saint-Louis

(2-LSL) reflect the impacts of the physical isolation of the 1-LSF created by the Moses–Saunders and the Beauharnois dams. It is clear that dams located on both sides of the 1-LSF have created a distinct water body characterised by altered connectivity, stabilised 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 et al., 2013; Holt et al., 2015). Downstream of Beauharnois dam, the hydrology gradually loses the imprints of water level regulation (Warwick & Dodson, 1999). Secondly, the complex mosaic of habitats in the archipelagos (*i.e.* Boucherville archipelago in the upper part of the 3-MS and 4-A-LSP) increases the specific diversity in the middle part of the St. Lawrence River. The 4-A-LSP hosts the richest (in rarefaction values) and the most diversified (in Simpson diversity values) fish communities. Thirdly, downstream sectors, marking the beginning of the mesotidal portion of the fluvial estuary, are home to distinct fish communities compared to the upstream part of the river (seen also by Leclerc & DesGranges, 2005). 6-BB and 7-GSN are composed of fluvial and estuarine species (e.g. *Microgadus tomcod*, *Acipenser oxyrinchus*, *Morone saxatilis*) due to their position along the longitudinal gradient. While only a few species were captured in 7-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 (e.g. *M. tomcod*) from the estuary bringing together distantly related species.

Longitudinal patterns from headwater toward the mouth were observed by several studies targeting small- to medium-sized rivers (e.g. Belliard et al., 1997; Bhat & Magnan, 2006; Araújo et al., 2009; Wu et al., 2011). In large rivers, such as the Ganges and the Mekong, the middle part of the river appears as the most diversified along the continuum when considering the specific fish diversity (e.g. Simpson diversity; Das et al., 2013; Chea et al., 2016). This pattern is also observed in the St. Lawrence River for Simpson

diversity and the rarefaction index (Fig. 2). The presence of phylogenetically distant estuarine and marine species observed in the lower part of large rivers is a likely reason explaining the local increase in taxonomic diversity at the end of the river continuum (i.e. river mouth).

Spatial heterogeneities at different scales

Even if both man-made longitudinal discontinuities (e.g. upstream dams) and riverscape heterogeneities are contributing to the longitudinal gradient observed in the St. Lawrence fish communities, a more complex and patchy organisation appears when considering the fish community at different spatial scales. As for results observed in the upper Mississippi (Chick et al., 2005), our results suggest a hierarchical structure of the spatial organisation in the St. Lawrence fish community. Firstly, contrasted hydro-geomorphological units along the river, such as the presence of a fluvial lake, largely increase habitat heterogeneity and 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 with limnophilic and vegetation-dependent species than corridor units typified by deep habitats and high current velocity with more rheophilic species (Leclerc & DesGranges, 2005).

Secondly, at sector scale ($\approx 15\text{--}50$ km), it appears that every sector identified according to their specific hydrological and morphometric characteristics hosted significantly distinct fish communities. Similar to the situation observed in the upper Paraná River (Agostinho et al., 2007; Ferrareze et al., 2014), our result confirms the importance of uniqueness in fluvial landscapes (Poole, 2002), which largely determine the fish community structure in large rivers. The types of spatial heterogeneity observed in each sectors such as the numerous islands and channels of the 4-A-LSP, the extensive floodplain of the 5-LSP, and the tidal movement in 7-GSN, appear as key elements structuring fish communities organisation of the St. Lawrence River.

Thirdly, when the heterogeneity of physical and biological conditions prevailing independently along either shore of a large temperate river are considered, such as in the St. Lawrence River, the global fish communities organisation revealed a much more

complex pattern. To our knowledge, large rivers have been never studied at the shore scale. However, this finer scale allowed highlighting similarities between adjacent sectors and transversal discontinuities within sectors in the St. Lawrence River. The 4-A-LSP and the nearby Maskinongé bay (see Fig. 1) identified as a productive habitat, seems to influence fish community structure of the upstream part of the 5-LSP, which contributes to fish community similarities along north shore (seine net results, Fig. 4). More surprisingly, the downstream part of the 5-LSP and the 6-BB sectors have similar communities (using the seine nets data) suggesting an higher homogeneity between these two sectors that previously expected considering that they are different hydro-morphological units. Since the 4-A-LSP and the 5-LSP are both considered highly productive areas (e.g. Tall et al., 2008; Mingelbier et al., 2016), they have the potential to “export” surplus production downstream (e.g. plankton; Basu et al., 2000) in sectors where emigrant fishes will eventually contribute to homogenise local communities. Moreover, results revealed differences between fish communities along north and south shores in several sectors of the St. Lawrence River. The local heterogeneity of habitats along each shore (e.g. watershed land use, hydro-geomorphology, tributaries, etc.), in some areas the large distance between opposing shores (e.g. ≥ 11 km in 2-LSL and 5-LSP) and, for several species, the large (≥ 300 m) and deep (≥ 8.2 m) navigation channel that may prevent fish dispersal (Leclerc & DesGranges, 2005; Leclerc et al., 2008) can account for the significant transversal differences observed in the St. Lawrence River. Even if the main channel can be a barrier for only some species (e.g. *Perca flavescens*, Leclerc et al., 2008) and not to the entire riverine specialists, the limited dispersal capacity of only a few species may change the overall community structure and diversity. Furthermore, the dominant land use in watershed and the water masses flowing along the north (suburban landscape, brown waters of the Ottawa River) and south shores (agricultural and industrial landscapes, green waters of the upper St. Lawrence River) of the 2-LSL are likely contributor to the perceived differences between northern and southern sector of the lake. Downstream in the 4-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 (Fig. 1). The Yamaska and

Saint-François tributaries drains polluted waters into the southern region of 5-LSP (MDDEP, 1998; Hudon & Carignan, 2008) which had deeply altered the vegetation (an important loss of the underwater vegetation). As the tributaries' waters did not cross the central navigation channel, they had not impacted the northern part of 5-LSP. Finally, the north shore of 6-BB is largely artificialized while the south shore is composed of large vegetated shoals similar to what was the 5-LSP until recently.

Implications for management

Unexpected diversity pattern

While considering the general spatial pattern of diversity, we identified two sectors exhibiting levels either much higher (i.e. 6-BB) or lower (i.e. 5-LSP) than expected (Mingelbier et al., 2008). Rarely considered as a hotspot for diversity, the little studied downstream Bécancour–Batiscau (6-BB) sector exhibits high values of rarefaction, Simpson diversity and taxonomic distinctness for both fish communities captured by seine net and gillnet (Fig. 2). The 6-BB is located downstream of the Lake Saint-Pierre (5-LSP), with large vegetated shoals along the southern shore. These results emphasise 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 5-LSP thanks to the sheer size of the area and the diversity of fish habitats it contains. The 5-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 community collected by seine net were lower than expected if LSP should be a hotspot of diversity (i.e. the LSP was not the richest and more diversified sector along the St. Lawrence River). Cumulative human pressures in the 5-LSP may partly explain this pattern. For example, the advent of intensive agricultural practices (e.g. corn and soy) on the 5-LSP floodplains has been identified as a primary cause for the collapse of the once locally super-abundant yellow perch (*Perca flavescens*; de la Chenelière et al., 2014).

Specific and Taxonomic diversity patterns

Specific and taxonomic diversity indices revealed different hotspots along the St. Lawrence River (e.g. 4-A-LSP and 7-GSN sectors). Since taxonomic diversity considers the evolutionary relationships within fish communities, it explicitly incorporates species differences rather than just the number of species that may be taxonomically redundant. In the St. Lawrence River, while the number of fish families observed in the 4-A-LSP is higher than in the 7-GSN sector, the elevated number of congeneric species in the 4-A-LSP (i.e. Cyprinidae, Centrarchidae and Percidae; Online Resource 3) lowers the value of the taxonomic diversity. For this reason, a higher taxonomical fish diversity is observed in the 7-GSN sector. Recognising the difficulties associated to decision-making when prioritising which areas should be protected in the face of limited financial resources, protecting the highest number of species possible without further consideration (e.g. ecological role, taxonomical redundancies, overall rarity, etc.) is not necessarily the most rewarding action; for the St. Lawrence River fishes community, the taxonomic distinctness appears as a measure worth further considerations (Vellend et al., 2011). Conversely, this index may be misleading as a seemingly “diversified” community may be the result of the combination of a few taxonomically divergent species. These perspectives underline the importance of considering simultaneously different measures of biodiversity in the overall evaluation of sites (e.g. richness species and taxonomic distinctness, Heino et al., 2005).

Management units

Management units have to be based on the structure of fish communities taking into account ecological gradients, discontinuities and heterogeneities. Even if hydro-morphological characteristics are useful to delineate functional management units in the St. Lawrence River (i.e. sector units; Mingelbier et al., 2016), other elements or processes such as human disturbances and fish dispersal can influence the fish community organisation. The differences between shores as well as the continuity observed between several sectors (i.e. 4-A-LSP/5-LSP and 5-LSP/6-BB) could 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 2-LSL were associated to the sedentary 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). Then, spatial processes observed at a broader scale (e.g. longitudinal dynamics) improve our understanding of how fish community is organised at the scale of the sector.

The usefulness of large and standardised sampling program

Only the system-wide, multiannual and standardised 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* (Online Resource 3). 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 River (i.e. 97 fish species) and accurately quantify densities for several species (e.g. *Anguilla rostrata*, lampreys, alosines, salmon, carps). For example, whereas millions of *Anguilla rostrata* have migrated in the St. Lawrence River (Guillemette et al., 2014), 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; La Violette et al., 2003; Mingelbier et al., 2016), 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 River.

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