# Beta diversity changes in estuarine fish communities due to environmental change

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ABSTRACT: Estuarine ecosystems are intrinsically resilient to the dynamic fluctuations of environmental conditions. Yet, it is unknown how the changes in environmental variability associated with climate change will affect fish communities. We assessed how species turnover over space and time in estuaries is influenced by changes in environmental conditions over years. We used fish abundances and water quality sampled at 42 stations among 7 estuaries in New Brunswick (Canada) from 2005 to 2012 to estimate (1) spatial turnover between stations based on the local contribution to beta diversity (LCBD) index, and (2) temporal turnover from year to year based on the β-Sørensen index. We found that beta diversity was potentially structured (i) over space due to inherent within-year differences in each estuary and (ii) over time related to the environmental condition of the previous year which led to changes in salinity, dissolved oxygen, and water temperature at sampling stations. Species contribution to spatial beta diversity (SCBD) was attributed across all years to 4 key species which were sensitive to dissolved oxygen. The current environmental condition of dissolved oxygen, temperature, salinity, and eelgrass *Zostera marina* affected temporal year-to-year turnover. When each year is analyzed separately, the estuaries with the greatest annual summer temperature fluctuations within a station contribute the most to spatial beta diversity between estuaries. Understanding how fish community structure responds to changes in environmental conditions can help inform the management of estuarine resources in the face of a rapidly changing environment.

KEY WORDS: Fish · Environmental change · Community ecology · Salinity · Temperature · Dissolved oxygen · Spatial beta diversity · Temporal beta diversity

## INTRODUCTION

In naturally dynamic systems such as estuaries, species are adapted to changing environmental conditions (Elliott & Whitfield 2011). Estuaries experience tidal and seasonal changes that lead to dramatic changes in salinity and temperature which fish species are able to survive by means of physiological and morphological adaptations (Cognetti & Maltagliati 2000, Elliott & Quintino 2007). While euryhaline species are adapted to tidal and seasonal salinity fluctuations, their response to greater temporal and spatial salinity changes due to climate change is unknown.

Climate change is expected to directly increase the variability and duration of changes in salinity, affecting the availability of suitable habitat for different spe-

cies (e.g. Robins et al. 2016). Extreme changes in salinity from intense precipitation and storm events have been predicted for the mid-Atlantic region of North America (Najjar et al. 2000). Other coastal marine ecosystems are already showing effects of low salinity due to freshwater inflow from flood events associated with snowmelt or rain events (H. Huang et al. 2014, W. Huang et al. 2014). In addition, long-term changes related to sea-level rises are anticipated to result in saltwater encroachment in coastal areas, including saltwater intrusion into freshwater aquifers further upstream (Werner & Simmons 2009, Hong & Shen 2012).

There may also be indirect effects of environmental changes to fish assemblages due to changes in water quality and the quality and quantity of fish habitat, such as eelgrass beds (*Zostera marina*). Eelgrass is particularly sensitive to salinity, with its niche of optimal salinity ranging between 20 and 26; however, salinity between 5 and 35 and even freshwater can be tolerated for brief periods (DFO 2009). Additionally, increases in magnitude and frequency of high (30°C) water temperature events increase the mortality of eelgrass in temperate estuaries, potentially past the point of recovery (Carr et al. 2012). Eelgrass beds provide structured habitat used by various invertebrate and fish species as spawning, nursery, and foraging grounds (Heck et al. 1995, DFO 2009). Thus, reducing the size and number of eelgrass beds due to unfavourable salinity and temperature conditions would indirectly affect fish communities by reducing prey abundance (i.e. invertebrates) and fish habitat (Boström & Bonsdorff 1997, Namba et al. 2018).

Fish community composition changes over space and time can be quantified using beta diversity (Whittaker 1972, Baselga 2010). Beta diversity can be partitioned as nestedness or turnover components (Baselga 2010). Nestedness can be used to describe species loss or compare species richness (Baselga 2010, Legendre 2014). Species turnover, also known as species replacement, along spatial and temporal gradients can be used to identify locations associated with greater environmental change (Baselga 2010). For example, these environmental gradients could be present in estuaries through salinity and temperature changes over space and time. Environmental processes, therefore, play a major role in turnover of fish assemblages in estuaries (Henriques et al. 2017).

Spatial gradients in salinity occur along estuaries due to freshwater input from watersheds upstream mixing with saltwater from the ocean. Salinity gradients and the effect on species assemblages have been assessed in large temperate estuaries with well-defined gradients, such as Chesapeake Bay, USA

(e.g. Jung & Houde 2003), the Severn, UK (e.g. Potter et al. 1986), and the Gironde, France (e.g. Pasquaud et al. 2012), as well as smaller estuaries such as those along the European Atlantic coast (e.g. Nicolas et al. 2010). In larger estuarine systems, spatial turnover of species communities is evident due to the defined salinity gradient (e.g. Wagner 1999, Martino & Able 2003, Giberto et al. 2007). Anthropogenic bathymetric changes to smaller estuaries have been shown to alter tides (e.g. Winterwerp et al. 2013). In smaller watersheds, the salinity gradient could be more sensitive to sudden changes from intense weather events and sea-level rise over a smaller area, but the extent of this effect is unknown. In fact, predicted climate change in eastern Canada is expected to impact all estuaries in the region with salinity and temperature changes (Zhang et al. 2000, Swansburg et al. 2004), and thus it is critical to determine the current structure of fish communities across smaller estuaries.

Here, our objective is to determine how fish communities in small, temperate estuaries are structured by environmental gradients over space and time in summer to facilitate predictions of changes that may be expected with climate change. We first determined how nektonic fish beta diversity varied with environmental changes over time from June to August 2005 to 2012 across a region of estuaries in the southern Gulf of Saint Lawrence, Canada. Second, we assessed which environmental variables are associated with beta diversity changes over space and time. Such analyses will provide a baseline of current fish community structure against which the effects of climate change may be detected.

## MATERIALS AND METHODS

### Study area

Our study comprised 7 temperate estuaries along the eastern coast of New Brunswick in the Northumberland Strait region of the southern Gulf of Saint Lawrence, Canada (46.1–47.8° N, 63.8–65.0° W; Fig. 1). The associated watersheds of the estuaries ranged from 150 to 510 km². Substrates in these estuaries are generally sand and mud and the predominant macrophyte is eelgrass *Zostera marina*.

### Sampling

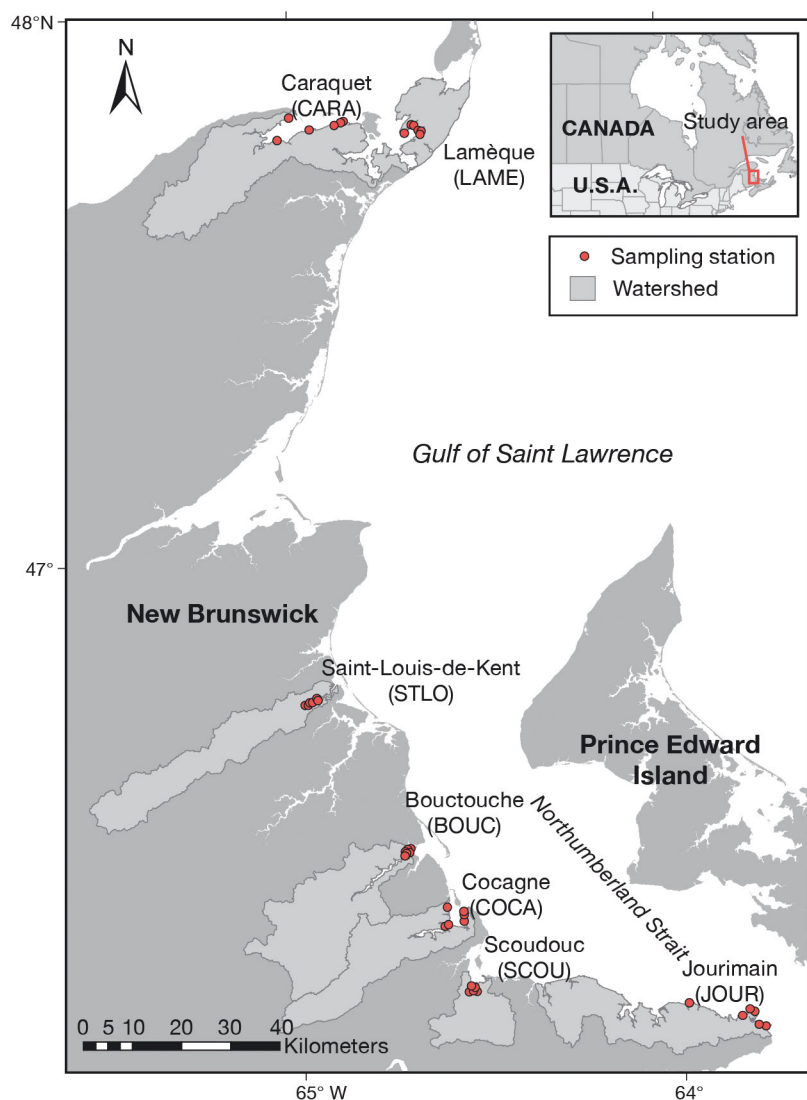We used fish and environmental data collected from the Community Aquatic Monitoring Program (CAMP),

Fig. 1. Study area and sampling stations (n = 42 stations) for the 7 estuaries and associated watersheds in New Brunswick (Canada)

month per station. Species were counted in a live box submerged in water and then released back into the estuary. Eelgrass coverage at each sample location was estimated using a 50 × 50 cm quadrat thrown randomly 3 times within the area seined. Eelgrass coverage is a score ranging from 0 to 5 from the quadrat sampling, with 0 as none and 5 indicating full coverage. At each station, water temperature, dissolved oxygen, and salinity were recorded using a portable meter (YSI Meter Model 85) at one-half to two-thirds of the depth down from the water surface and ca. 7 m from shore in the beach seine area. Tidal stage during a sampling event was recorded and 5 levels distinguished: high tide, incoming, mid-tide, outgoing, or low tide.

## Beta diversity

Beta diversity is a measure used to compare variations in species composition over space and time as species nestedness or species turnover (Baselga 2010). Using species turnover (replacement), we partitioned total spatial beta diversity in 2 ways (Legendre & De Cáceres 2013). First, spatial beta diversity was calculated based on the local contribution to beta diversity (LCBD) index that assesses which stations contribute the most to spatial beta diversity among all 42 stations (7 estuaries and 6 stations per estuary) using the overall average abundance of species from 2005 to 2012. LCBD represents the uniqueness of community composition in sampling stations across the sampling region (Legendre & De Cáceres 2013). LCBD was then calculated over the 42 stations for each year separately. Second, species that contribute the most to spatial beta diversity each year can be assessed using the species contribution to beta diversity (SCBD; Legendre & De Cáceres 2013). Before running the analyses for LCBD and SCBD, we applied a Hellinger transformation to the abundance data so that beta diversity values could be computed (Legendre & De Cáceres 2013). Temporal turnover was measured using the Sørensen pairwise beta diversity (β-Sørensen; Baselga 2010) index comparing year-to-year

which is coordinated by the Southern Gulf of St. Lawrence Coalition on Sustainability and Fisheries and Oceans Canada (Weldon et al. 2005). Adult fish sampled once monthly in June–August 2005–2012 by beach seine (30 × 2 m; 6 mm mesh) were enumerated by species at 6 fixed sampling stations within each estuary (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m603p161_supp.pdf). Fish communities at each station were summarized by the annual average catch of all months. Sampling stations were chosen within comparable estuaries but stations themselves varied in nature so as to span a range of environmental gradients and macrophyte vegetation. Given that each location is different in terms of bathymetry, the target sampling area encompassed a 15 × 15 m block bordering the shore with 1 sample each

turnover considering all the 42 sampling stations, for each sampling station from 2005 to 2012.

## Relationship of beta diversity to environmental conditions

We determined periods of significant environmental change during our study period from 2005 to 2012. Significantly different years of salinity, water temperature, and dissolved oxygen were assessed using ANOVA. We further investigated the potential effect of the tidal cycle on salinity for each year associated with the timing of sampling during tides by performing a 2-way ANOVA (factors are tidal stage: high tide, incoming, mid-tide, outgoing, low tide; and year). Significant year-to-year differences in the amount of eelgrass coverage were not calculated as this was based on random quadrats rather than resampled quadrats.

We assessed which environmental variables as predictors affect beta diversity (spatial turnover response variable is LCBD and temporal turnover is β-Sørensen where each sample in the data matrix is 1 site in 1 year) in our study using generalized linear mixed models (GLMMs) with Gaussian error distribution due to the normal distribution of data. Normality was verified with Q-Q plots and collinearity between environmental variables was checked with a Pearson correlation matrix. To model temporal turnover in species composition (here measured with β-Sørensen between consecutive years), we built 2 alternative models with the current year (current env.) and the previous year (lag env.) as predictor variables. We were interested in determining which year of the turnover difference had a greater influence on species composition changes over time. The current year of environmental condition (current env.) refers to the end of each year-to-year turnover, whereas the time lag refers to the beginning of each year-to-year turnover (lag env.). Overall, the current year of environmental condition refers to the time period from 2006 to 2012 and the lag year of environmental condition refers to the time period from 2005 to 2011. Fixed factors were environmental and habitat variables such as salinity, dissolved oxygen, temperature, and eelgrass coverage. We further analyzed within-year variability at each station by determining the interquartile ranges (IQR) for environmental condition as a fixed factor. Each estuary had variable levels of fluctuations of salinity from 2005 to 2012 (Fig. S1 in Supplement 2). Estuaries of the sampling stations were treated as random factors to ac-

count for the potential spatial effect of a group of stations within the same estuary on the response variable. From a full model containing all of the fixed factors, we constructed reduced models with all possible combinations of the variables based on Akaike's information criterion (AIC; Burnham & Anderson 2002). We compared the full model with the reduced model using a chi-squared test. We performed bootstrapping of the best reduced models with 200 replications to determine the 95% confidence intervals (CI) of fixed factors. If the 95% CI did not overlap with 0, then the fixed factor was considered to have a significant effect on the response variable. $R^2$ values were calculated to determine the variance explained by the best reduced model based on the methods described in Nakagawa & Schielzeth (2013). We then calculated $R^2_{GLMM(m)}$, which is the marginal $R^2$ pertaining to the variance explained by fixed factors, and $R^2_{GLMM(c)}$, which is the conditional $R^2$ pertaining to the variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013).

We assessed which environmental variables as predictors affect SCBD with each entry in the data matrix as each year using generalized linear models (GLMs) for Gaussian (normal) data. We checked for normality and removed predictors that are collinear, which reduced it to 4 predictor variables: dissolved oxygen, dissolved oxygen IQR, salinity IQR, and temperature IQR. To model SCBD each year, we built 2 alternative models with the current year (current env.) and the previous year (lag env.) as predictor variables. The current year of environmental condition spans from 2006 to 2012. The previous year of environmental condition spans from 2005 to 2011. Due to small sample sizes, we compared models with AIC corrected for small sample sizes (AIC$_c$; Burnham & Anderson 2002).

All analyses were performed using the program R, version 3.1.0 (R Core Team 2014). We partitioned beta diversity into turnover using the betapart package in R (Baselga et al. 2013). We analyzed LCBD and SCBD values using the beta.div package from Legendre & De Cáceres (2013). GLMMs were constructed using the lme4 package from Bates et al. (2015).

## RESULTS

### Fish species

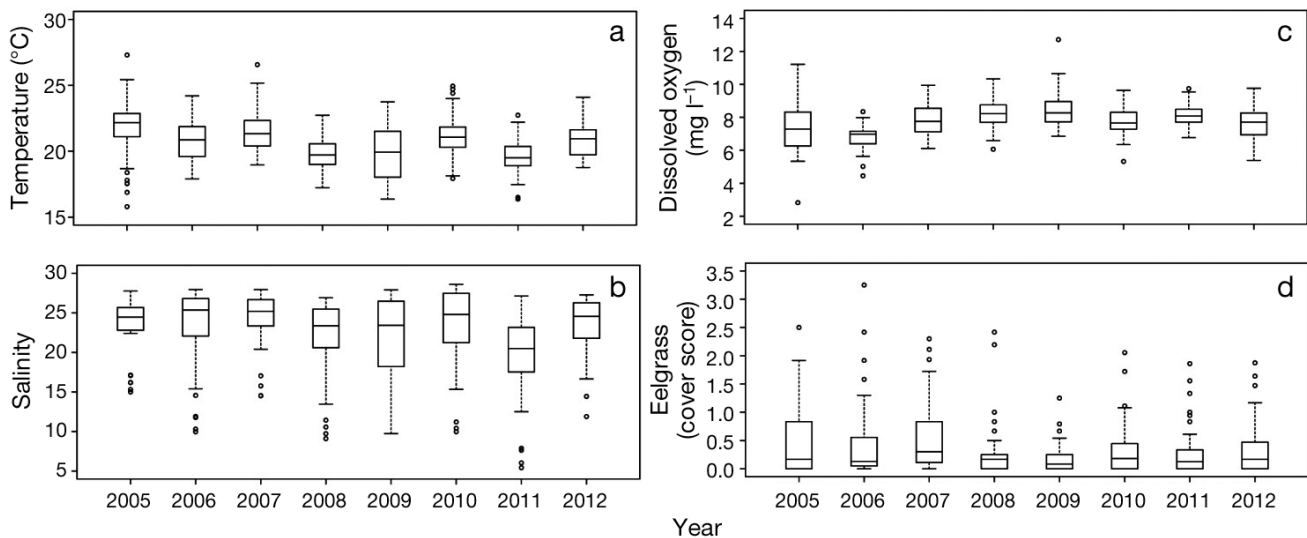The CAMP detected 26 species of adult fish across the 7 focal estuaries (Table S1 in Supplement 1).

Fig. 2. Boxplot of water temperature, salinity, dissolved oxygen, and eelgrass coverage within stations in the 7 focal estuaries (n = 42 stations each year) from June to August of 2005 to 2012. Box: interquartile range (IQR), vertical bars: minimum and maximum; horizontal line within the box: median. Outliers (circles) are 1.5 × IQR. Eelgrass coverage is a score (0–5) from the quadrat sampling, with 5 indicating full coverage

Over all months (June, July, August) and years (the 8 years 2005–2012) sampled, the number of species ranged from 6 to 17 per sampling station.

### Environmental condition

Water temperature varied from a minimum of 15.8°C to maximum 27.3°C from 2005 to 2012 (Fig. 2a). The lowest water temperature was recorded in Jourimain and the highest was in Cocagne, both in 2005. Water temperature varied significantly across 2005 to 2012 ($F_{7,328}$ = 11.4, p < 0.001; Fig. 2a), with a significant decrease from 2007 to 2008 (p < 0.001; Fig. 2a). There was a significant increase in water temperature from 2009 to 2010, followed by a significant decrease from 2010 to 2011, and finally a significant increase from 2011 to 2012 (all p < 0.001; Fig. 2a). Within-year variability of water temperature IQR at each station differed between 2005 and 2012 within the 42 stations ($F_{7,328}$ = 8.2, p < 0.001), with 2010 to 2011 being the only 2 consecutive years that showed a significant difference (p < 0.001).

Annual mean salinity fluctuated from a minimum of 5.4 to maximum 28.6 from 2005 to 2012 (Fig. 2b). The lowest salinity was recorded in Saint-Louis-de-Kent in 2011, in contrast to the highest salinity in Lamèque during 2010 (Fig. S1 in Supplement 2). Significant variation occurred for salinity across 2005 to 2012 ($F_{7,328}$ = 4.3, p < 0.001; Fig. 2b). Recorded salinity dropped significantly from 2007 to 2008 and 2010

to 2011, and increased from 2011 to 2012 (all, p < 0.001; Fig. 2b). Salinity IQR varied significantly across 2005 to 2012 ($F_{7,328}$ = 5.5, p < 0.001), although only marginally from 2007 to 2008 (p = 0.056). We found that there was a significant effect of the tidal cycle (5 levels as defined in 'Materials and methods') on salinity during the 8 sampling years (2005 to 2012) using a 2-way ANOVA ($F_{23,765}$ = 3.437, p < 0.001; in some years, sampling did not always occur during a specific tidal cycle). Furthermore, although there was a significant effect based on the sampling done during a specific tidal cycle, a post hoc analysis of this interaction was only significantly different from 2005 to 2006 (Tukey post hoc test: p < 0.001). Therefore, the majority of years, with the exception of 2005 to 2006, were sampled across all tidal cycles to capture the environmental change in salinity.

Dissolved oxygen varied from 2.8 to 12.7 mg l⁻¹ (Fig. 2c). Dissolved oxygen varied significantly across 2005 to 2012 ($F_{7,328}$ = 10.3, p < 0.001; Fig. 2c), whereby 2006 was significantly lower than 2007 (p < 0.001) and 2011 was significantly higher than 2012 (p < 0.001; Fig. 2c). The lowest levels of dissolved oxygen were found in Lamèque during 2005, and the highest levels were found in Bouctouche during 2008. Dissolved oxygen IQR varied significantly from 2005 to 2012 ($F_{7,328}$ = 2.8, p = 0.007), with 2011 to 2012 being the only 2 consecutive years that showed a significant difference (p = 0.003).

Between 2005 and 2012 eelgrass was absent (i.e. it had an annual average score of 0) in a total of 113

observations at 39 stations within the 7 estuaries (Fig. 2d). The maximum annual average score for eelgrass coverage was 3.25 at Caraquet in 2006.

## Spatial beta diversity

LCBD values measured across all years ranged from 0.005 to 0.0418, and we found 4 sampling stations that had significant LCBD values (Fig. 3). These significantly different sites were found within the estuaries of Saint-Louis-de-Kent and Cape Jourimain. When the LCBD was calculated each year from 2005 to 2012 for the 42 stations, stations in Jourimain contributed to beta diversity every year (Fig. S2 in Supplement 3).

We found 6 species contributing greater than the overall mean beta diversity (SCBD) value (0.037; Table 1) considering all years from 2005 to 2012. SCBD values ranged from 0 to 0.227 (Table 1). Four species contributed greater than the mean beta diversity across all stations obtained considering all years from 2005 to 2012 (Table 1). A total of 9 different species contributed greater than the mean beta diversity value in any 1 year (Table 1).

## Temporal beta diversity

Temporal turnover considering all stations measured as β-Sørensen of year-to-year changes in community composition was significantly different from 2005 to 2012 ($F_{6,246} = 316.9$, p < 0.001). All year-to-year comparisons were significantly different (after Bonferroni correction: p < 0.001), with the exceptions of 2008–2009 and 2009–2010 (Bonferroni correction: p > 0.05). Two periods, 2006–2007 and 2011–2012, showed markedly low temporal turnover, in contrast to 2005–2006, with high temporal turnover (Fig. 4). Overall, temporal turnover considering all stations responded similarly over time between stations and among estuaries (Fig. 4).

## Relationship of beta diversity to environmental change

The reduced GLMM with estuaries as a random effect for the LCBD values contained only temperature IQR (Table 2). The full model was not significantly different than the reduced model with temperature IQR ($\chi^2 = 2.98$, df = 7, p = 0.89). The reduced model explained 43.3% of the variation ($R^2_{GLMM(c)}$) of LCBD values, temperature IQR explained 0.08% of the variation ($R^2_{GLMM(m)}$), and estuaries as a random effect explained 43.22% of the variation.
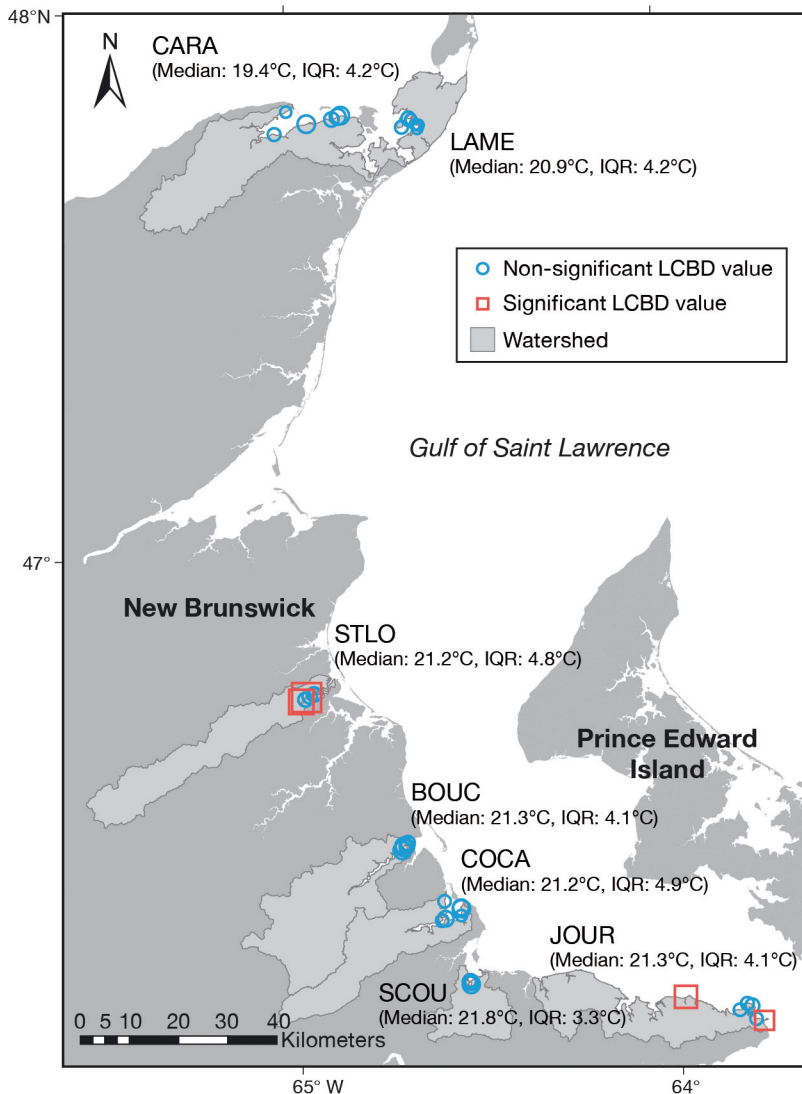


Fig. 3. Local contribution to spatial beta diversity (LCBD) represented as relative proportional symbols and significant sites across 42 sampling stations considering all years (2005–2012). Higher LCBD values indicate greater differences in community composition at a site compared to all sites in a region. Maximum LCBD value is 0.0418. Significant sites contributing to beta diversity located in STLO and JOUR. Median and interquartile range (IQR) of summer water temperature within each estuary is marked. See Fig. 1 for abbreviations of estuaries

Table 1. Species contribution to spatial beta diversity (SCBD) across 42 sampling stations in each year from 2005 to 2012 and the associated ranks of the highest SCBD values for each year. Bolded mean SCBD values indicate species contributing greater than the mean SCBD across all stations considering all years from 2005 to 2012 (mean = 0.0370), and bolded ranks indicate years when SCBD was greater than mean SCBD. Mean abundance of species averaged for each year from 2005 to 2012 across 42 sampling stations

| Common name | Scientific name | Mean SCBD | Mean abundance | SCBD rank by year | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 |
| Mummichog | *Fundulus heteroclitus* | **0.227** | 135.1 | **3** | **2** | **1** | **1** | **2** | **1** | **1** | **1** |
| Atlantic silverside | *Menidia menidia* | **0.212** | 80.2 | **1** | **1** | **2** | **4** | **4** | **2** | **2** | **2** |
| Fourspine stickleback | *Apeltes quadracus* | **0.168** | 37.9 | **2** | **3** | **3** | **2** | **1** | **3** | **3** | **3** |
| Threespine stickleback | *Gasterosteus aculeatus* | **0.161** | 40.5 | **4** | **6** | **4** | **3** | **3** | **4** | **4** | **5** |
| Blackspotted stickleback | *Gasterosteus wheatlandi* | **0.061** | 17.0 | **5** | **4** | 7 | **5** | **5** | **6** | **6** | **4** |
| Banded killifish | *Fundulus diaphanus* | **0.044** | 6.2 | 9 | 11 | 8 | 11 | 11 | 8 | **7** | 8 |
| Ninespine stickleback | *Pungitius pungitius* | 0.035 | 5.3 | **6** | **7** | **6** | **7** | **7** | **7** | 8 | 9 |
| Smooth flounder | *Pleuronectes putnami* | 0.033 | 3.2 | 8 | **5** | **5** | **6** | **6** | **5** | **5** | **6** |
| Alewife | *Alosa pseudoharengus* | 0.03 | 1.3 | 16 | 18 | 17 | 15 | 9 | 11 | 20 | **7** |
| Winter flounder | *Pseudopleuronectes americanus* | 0.007 | 0.7 | **7** | 9 | 10 | 10 | 10 | 9 | 9 | 10 |
| American sand lance | *Ammodytes americanus* | 0.006 | 0.09 | 15 | 12 | 15 | **8** | 8 | 21 | 12 | 13 |
| Cunner | *Tautogolabrus adspersus* | 0.004 | 0.08 | 11 | 14 | 13 | 16 | 19 | 13 | 13 | 11 |
| Striped bass | *Morone saxatilis* | 0.004 | 0.1 | 18 | 18 | 17 | 9 | 17 | 14 | 10 | 18 |
| Rainbow smelt | *Osmerus mordax* | 0.002 | 0.03 | 17 | 18 | 17 | 21 | 16 | 15 | 20 | 14 |
| Northern pipefish | *Syngnathus fuscus* | 0.002 | 0.08 | 18 | 8 | 14 | 21 | 19 | 12 | 15 | 22 |
| Windowpane flounder | *Scophthalmus aquosus* | 0.001 | 0.02 | 10 | 18 | 11 | 13 | 14 | 10 | 16 | 12 |
| Atlantic tomcod | *Microgadus tomcod* | 0.001 | 0.08 | 12 | 10 | 9 | 14 | 13 | 19 | 11 | 15 |
| Grubby | *Myoxocephalus aenaeus* | 0.001 | 0.01 | 18 | 18 | 17 | 21 | 19 | 18 | 20 | 17 |
| American eel | *Anguilla rostrata* | 0 | 0.03 | 13 | 13 | 17 | 18 | 12 | 16 | 14 | 20 |
| Shorthorn sculpin | *Myoxocephalus scorpius* | 0 | 0.01 | 14 | 17 | 12 | 20 | 19 | 21 | 17 | 19 |
| Lake chub | *Couesius plumbeus* | 0 | 0.003 | 18 | 15 | 17 | 21 | 19 | 21 | 20 | 24 |
| Trout spp. | | 0 | 0.001 | 18 | 16 | 16 | 21 | 19 | 21 | 20 | 24 |
| Rock gunnel | *Pholis gunnellus* | 0 | 0.007 | 18 | 18 | 17 | 12 | 18 | 17 | 20 | 23 |
| White sucker | *Catostomus commersonii* | 0 | 0.0008 | 18 | 18 | 17 | 17 | 19 | 21 | 18 | 24 |
| Brook trout | *Salvelinus fontinalis* | 0 | 0.007 | 18 | 18 | 17 | 19 | 15 | 20 | 18 | 21 |
| Cyprinidae family | | 0 | 0.0004 | 18 | 18 | 17 | 21 | 19 | 21 | 20 | 16 |

For temporal turnover (β-Sørensen) considering all stations with year-to-year variation of species communities and the current year for environmental condition as fixed effects and estuaries as a random effect, the reduced model contained dissolved oxygen, temperature, salinity, dissolved oxygen IQR, and eelgrass (Table 2). The full model was not significantly different than the reduced model ($\chi^2$ = 1.70, df = 3, p = 0.64). The reduced model explained 11.7% of the variation ($R^2_{GLMM(c)}$) of β-Sørensen values, all due to environmental condition.

For the time lag of 1 yr for environmental condition and its effect on β-Sørensen values, the reduced model with estuaries as a random effect contained salinity IQR, temperature IQR, dissolved oxygen IQR, and temperature (Table 2). The time lag of 1 yr for the effect of temperature on temporal turnover was not significant (Table 2). The reduced model was not significantly different than the full model ($\chi^2$ = 1.91, df = 4, p = 0.75). The reduced model explained 23.0% of the variation ($R^2_{GLMM(c)}$). The fixed factors explained 21.8% of the variation ($R^2_{GLMM(m)}$), and the random effect of estuaries explained 1.2% of the variation.

SCBD each year was affected by the current environmental condition of dissolved oxygen from 2006 to 2012 (Table 3). The 4 species that responded to dissolved oxygen (Table 3) also corresponded to the species that consistently contributed to beta diversity greater than the mean SCBD between stations considering all years from 2005 to 2012 (Table 1). Mummichog *Fundulus heteroclitus* and Atlantic silverside *Menidia menidia* contributed less to beta diversity with increasing dissolved oxygen, whereas fourspine stickleback *Apeltes quadracus* and threespine stickleback *Gasterosteus aculeatus* contributed more to beta diversity with increasing dissolved oxygen. By contrast, SCBD was unaffected by the environmental condition of the previous year, as none of the variables were significant.

## DISCUSSION

We found that the amount of eelgrass, salinity, water temperature, and dissolved oxygen gradients over time are related to the environmental condition
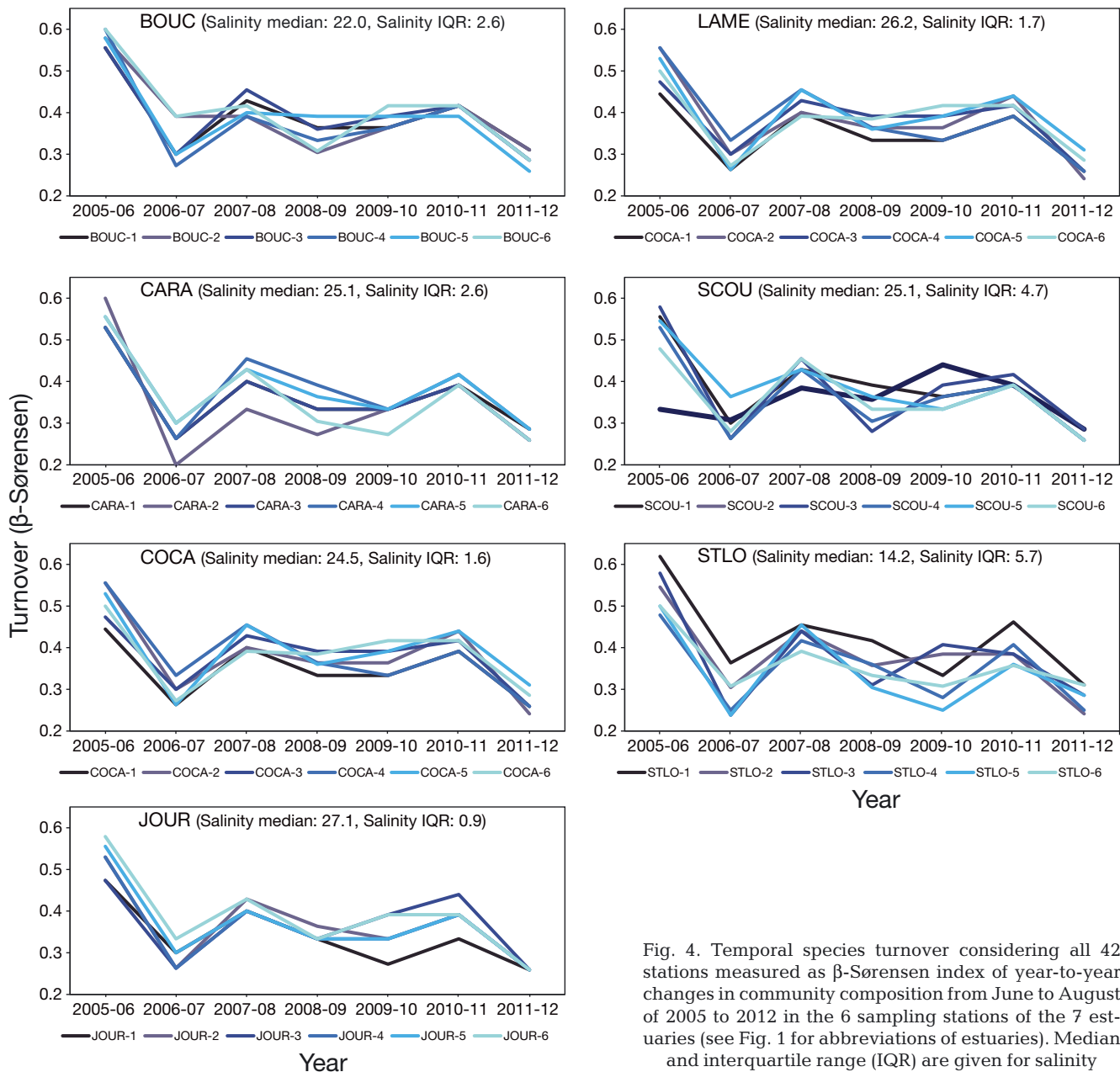
Fig. 4. Temporal species turnover considering all 42 stations measured as β-Sørensen index of year-to-year changes in community composition from June to August of 2005 to 2012 in the 6 sampling stations of the 7 estuaries (see Fig. 1 for abbreviations of estuaries). Median and interquartile range (IQR) are given for salinity

leading to temporal turnover as fish composition changes. Previously, it has been shown that other seagrasses in estuaries are sensitive to extreme fluctuations in salinity and water temperature (e.g. Montague & Ley 1993, Glemarec et al. 1997, Fernández-Torquemada & Sánchez-Lizaso 2005). Consequently, the increased mortality of seagrasses leads to greater decay of organic matter, thus reducing dissolved oxygen levels through the decomposition of detritus (D′Avanzo et al. 1996). Due to these changing dissolved oxygen levels and reduction in habitat in estuaries, temporal turnover occurs as species are re-

placed by persistent species that can tolerate lower oxygen conditions (Pihl et al. 1991).

Spatial turnover of each year measured as the LCBD index was mostly influenced by specific characteristics of each estuary (random effect explained 43.22% of the variance) that in turn potentially influence environmental variation. Such characteristics of estuaries could be due to the bathymetry and exposed or sheltered estuaries affecting fish communities within and across estuaries (Lekve et al. 2002). Thus, unmeasured geomorphological differences within an estuary may have resulted in the variability of

Table 2. Generalized linear mixed effect models (GLMMs) for beta diversity as a response to the effects of significant (p < 0.05) annual environmental variables from 2005 to 2012 in 42 stations, with model coefficient and confidence intervals (CI). Spatial turnover analyzed as local contribution to beta diversity (LCBD). Temporal turnover (β-Sørensen index) of year-to-year variation analyzed with the environmental condition of the current year (current env.) and a time lag of 1 yr (lag env.). Estuaries (n = 7) were treated as a random effect. $R^2_{GLMM(c)}$: conditional $R^2$ (variance explained by fixed and random effects), $R^2_{GLMM(m)}$: marginal $R^2$ (variance explained by fixed effects), IQR: interquartile range

| Response | Variable | Estimate | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|
| | Random effect (spatial): Estuaries (n = 7 yr) | | | |
| **LCBD (spatial turnover)** (n = 336, $R^2_{GLMM(c)}$ = 0.433, $R^2_{GLMM(m)}$ = 0.0008) | | | | |
| | Temperature IQR | 0.015 | 0.0082 | 0.022 |
| **β-Sørensen (temporal turnover, current env.)** (n = 294, $R^2_{GLMM(c)}$ = 0.117, $R^2_{GLMM(m)}$ = 0.117) | | | | |
| | Dissolved oxygen | 0.53 | 0.47 | 0.62 |
| | Temperature | 0.48 | 0.36 | 0.61 |
| | Salinity | 0.41 | 0.37 | 0.46 |
| | Dissolved oxygen IQR | 0.38 | 0.36 | 0.40 |
| | Eelgrass | 0.37 | 0.36 | 0.38 |
| **β-Sørensen (temporal turnover, lag env.)** (n = 294, $R^2_{GLMM(c)}$ = 0.230, $R^2_{GLMM(m)}$ = 0.218) | | | | |
| | Salinity IQR | 0.42 | 0.39 | 0.45 |
| | Temperature IQR | 0.38 | 0.36 | 0.41 |
| | Dissolved oxygen IQR | 0.36 | 0.34 | 0.37 |
| | Temperature | 0.062 | −0.039 | 0.18 |

Table 3. Generalized linear models (GLMs) for 4 species' contribution to beta diversity (SCBD) annually as a response to the effects of significant annual environmental variables (current environmental condition) averaged across 42 stations each year from 2006 to 2012 (n = 7). Model coefficients, standard error (SE), and p-values of the best supported model for each species are displayed

| SCBD | Parameter | Estimate | SE | p |
|---|---|---|---|---|
| Mummichog | Intercept | 0.66 | 0.14 | 0.006 |
| *Fundulus heteroclitus* | Dissolved oxygen | −0.054 | 0.019 | 0.03 |
| Atlantic silverside | Intercept | 0.86 | 0.17 | 0.004 |
| *Menidia menidia* | Dissolved oxygen | −0.083 | 0.022 | 0.01 |
| Fourspine stickleback | Intercept | −0.14 | 0.086 | 0.16 |
| *Apeltes quadracus* | Dissolved oxygen | 0.039 | 0.011 | 0.02 |
| Threespine stickleback | Intercept | −0.44 | 0.11 | 0.01 |
| *Gasterosteus aculeatus* | Dissolved oxygen | 0.072 | 0.014 | 0.004 |

spatial turnover among other estuaries. Once the effects of each estuary are accounted for, there is evidence that the variability of water temperature affects spatial turnover of each year (fixed effect significantly explained 0.08% of the variance).

By contrast, temporal turnover of year-to-year variation in fish communities was mostly driven by water temperature, salinity, the amount of eelgrass, and dissolved oxygen during the current year of environmental condition in all estuaries. The environmental condition of a time lag of 1 yr contributed to temporal turnover due to variability of salinity, temperature, and dissolved oxygen. Furthermore, locations along

a geographical region, here based on the estuary, affected temporal turnover each year. Each individual estuary had different environmental gradients and variability over space and time that could be influenced by the shape and size of the estuary. For example, smaller and broader estuaries would potentially have shorter environmental gradients of temperature compared to larger and longer estuaries. These differences may contribute to the magnitude of change of environmental condition within each estuary. Therefore, spatial and temporal turnover of fish communities may be driven by environmental changes in our study area.

Dissolved oxygen during a given current year of environmental condition affects year-to-year temporal turnover. During the study period, dissolved oxygen in the estuaries fluctuated to levels below 8.0 mg l⁻¹. The interim recommended guideline for dissolved oxygen in estuarine waters is a minimum of 8.0 mg l⁻¹ or lower if natural processes resulted in this decrease (Canadian Council of Ministers of the Environment 1999). Given that the estuaries within this study area fluctuated below the interim guideline, the lower dissolved oxygen levels may be due to eutrophication caused by potential anthropogenic impact in several of the estuaries of New Brunswick (Schmidt et al.

2012). In contrast to the Canadian Council of Ministers of the Environment (1999) recommended interim guideline of 8.0 mg l$^{-1}$, several studies have recommended lower thresholds for aquacultures in coastal waters (e.g. Brooks & Mahnken 2003, Page et al. 2005). The effects of hypoxic conditions begin to affect the metabolism of species between 2.0 and 4.0 mg l$^{-1}$, and mortality occurs below 0.5–2.0 mg l$^{-1}$ (Gray et al. 2002, Vaquer-Sunyer & Duarte 2008). Prolonged variability away from the norm would favour species tolerance of lower dissolved oxygen levels and ultimately a shift in assemblage composition.

Changes in species composition over time, and measured as SCBD, were attributed to 4 key species across all years: mummichog *Fundulus heteroclitus*, Atlantic silverside *Menidia menidia*, fourspine stickleback *Apeltes quadracus*, and threespine stickleback *Gasterosteus aculeatus*. Species able to tolerate a wide range of environmental conditions, such as *F. heteroclitus*, contributed to beta diversity between stations in all years. *F. heteroclitus* is known to be tolerant to environmental changes such as fluctuating temperatures, salinity, and low levels of dissolved oxygen as well as pollutants (Abraham 1985, Marshall et al. 1999, Weis 2002, Stierhoff et al. 2003). Given that *F. heteroclitus* is adapted to low dissolved oxygen, it would contribute more to beta diversity during these periods. Due to the turnover of other species unable to tolerate lower dissolved oxygen, *F. heteroclitus* becomes abundant at particular sites. For example, sites that are impacted by anthropogenic activities, such as agriculture, with signs of eutrophication and showing hypoxic conditions, tend to be dominated by *F. heteroclitus* (Finley et al. 2009). The dominance of *F. heteroclitus* during these conditions may be due to their ability to gulp air at the water surface and thereby survive low oxygen conditions (Stierhoff et al. 2003). In contrast to hypoxic conditions, the dominance of *F. heteroclitus* would be reduced during normoxic conditions. Despite these periods of prominent environmental change, *F. heteroclitus* is able to persist and remains as an important part of the community composition in estuaries.

Similarly, the lower dissolved oxygen during sampling in 2008 resulted in species such as *M. menidia* contributing more to beta diversity between stations during that year. During spawning, *M. menidia* have been found congregating in areas with depleted dissolved oxygen (Middaugh et al. 1981). The spawning season for *M. menidia* in higher latitudes begins in early summer (Middaugh 1981, Conover & Present 1990), which coincides with the sampling period of our study. As a result of the greater abundance of *M.*

*menidia* associated with periods of low dissolved oxygen, SCBD is higher during these events.

Demersal species in the Gasterosteidae family responded to high dissolved oxygen. *A. quadracus* and *G. aculeatus* were sensitive to dissolved oxygen when these species were found in greater abundance and contributed to beta diversity. Eggs of *A. quadracus* have greater mortality in periods of low dissolved oxygen, which reduces the recruitment to the adult population (Poulin & FitzGerald 1989). *G. aculeatus* has also been associated with high dissolved oxygen in European estuaries (Araújo et al. 1999, Maes et al. 2007). Thus, when looking at the respective current environmental condition of year-to-year changes in species composition, dissolved oxygen is an important factor in structuring turnover.

Results of our analysis with 1 yr lag indicate that greater within-year variability of environmental conditions, specifically salinity, temperature, and dissolved oxygen, have an effect on temporal species turnover. Yet, species communities are also rapidly responding to the current environmental conditions based on the temporal turnover in the respective year. We found that the locations that affect spatial beta diversity the most were consistent across the years, such as sampling stations within Cape Jourimain located on the coast. These exposed stations allow for greater flushing, resulting in consistent fish habitat over years (Nedwell 1996).

We focused on the lag of environmental conditions, as we were interested in the effects of the environmental conditions of the previous year. The lag response of fish species turnover to environmental conditions may be due to the recruitment of adult individuals. Unfavourable environmental conditions during a year may then be linked to changes in trophic interactions of fish communities or adult condition (Neill et al. 1994, Pershing et al. 2005), leading to lower fecundity for adult individuals and therefore reducing recruitment in subsequent years. It is necessary to distinguish this lag of environmental condition from the magnitude of environmental change between years. Henriques et al. (2017) assessed the environmental dissimilarity between fish communities in estuaries worldwide, where environmental differences such as sea surface temperature structure fish species turnover. These differences within environmental gradients may elucidate how fish communities respond in estuaries. Here, we found that the environmental variability within a year, which is different than the magnitude of difference between years, also causes spatial and temporal fish species turnover in estuaries.

Spatial turnover considering all years does not change rapidly over time, as communities are mainly structured by the robust environmental gradients that occur within each estuary. These salinity gradients structure fish communities in large estuaries such as Chesapeake Bay (Jung & Houde 2003), as well as small estuaries (e.g. Harrison & Whitfield 2006, Nicolas et al. 2010). Turnover in fish communities has been examined in a wide range of estuaries globally (Henriques et al. 2017), and in upstream freshwater environmental gradients (Edge et al. 2017). Similarly, we have also found that temperature gradient changes in the smaller estuaries of New Brunswick may structure fish community turnover. These variations may be driven by individual estuaries due to unmeasured parameters such as bathymetry, as our results indicate that each estuary had a prominent effect on spatial turnover. For example, the species assemblage of our Cape Jourimain site contrasts significantly with other sites in the region, as it is exposed to the sea. Second, the watersheds of the estuaries could contribute to the environmental variation affecting submergent aquatic vegetation (Li et al. 2007), which may indirectly affect fish assemblages. Future research into the bathymetry and the watersheds of the estuaries could potentially drive the environmental variation influencing spatial and temporal turnover of fish communities.

In summary, spatial turnover operates on a localized scale corresponding to each estuary where environmental variability remains an important factor that influences the structure of fish community composition in the dynamic nature of estuaries. Effects of large-scale changes, such as climate change leading to increased within-year variability, could have potential effects on localized changes in estuaries that affect species composition over time. These findings imply that temporal turnover is rapid in estuaries, due to environmental variability, and shifts in species communities that occur during the year are due to sensitivity to environmental change. As a result, such climatic changes would undermine any management efforts regarding the reduction of anthropogenic pressures in estuarine ecosystems.

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