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Estuarine lateral ecotones shape taxonomic and functional structure of fish assemblages. The case of the Seine Estuary, France

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ABSTRACT

Estuaries are complex ecotones including multiple lateral habitats that play essential functions for fish assemblages. However, the distribution of fish diversity and community assembly processes remain poorly documented in these habitats. This paper investigated the taxonomic and functional diversities of fish assemblages along lateral continuums of three salinity areas over the longitudinal gradient of the Seine Estuary. We examined fish diversity at a local scale (α -diversity) and between local scales (β -diversity) across the lateral habitats (estuarine main channel, tidal marsh, and diked marsh). Overall, the taxonomic diversity follows a typical ecotone distribution, with the highest richness reported at the system margins and high species dissimilarity between communities. The decrease of functional diversity in upper part of the lateral ecotone probably reflects the homogenisation of ecological niches. Changes in assembly processes between the three salinity conditions suggests that several lateral ecotones occur in estuaries with complementary functions for fish assemblages.

1. Introduction

Transitional areas between contrasted ecological regions or ecosystems can be characterised as ecotones. These areas, which can occur at large or local spatial scales, are often associated with strong environmental shifts along ecological gradients (Kark, 2013). They represent locations of strong interactions between contrasted communities (Kent et al., 1997) with a high rate of changes in structure or ecological functions (Di Castri et al., 1988). Such processes can be highlighted by investigating the β -diversity, which attempts to measure the extent of compositional differences between ecological assemblages. Beta diversity can be partitioned in two different components, i.e., turnover and nestedness (Baselga, 2010; Legendre, 2014). Turnover denotes dissimilarity pattern where some species replace others as a consequence of environmental sorting and/or spatial and historical constraints (Leprieur et al., 2009). Turnover can be distinguished from nestedness, which reflects a non-random process of species loss along gradients where the poorest assemblage is a subset of the richest assemblage (Ulrich et al., 2009). This pattern is expected to result from various mechanisms such as selective colonisation, habitat nestedness, or differential species loss related to their environmental tolerance (Leprieur et al., 2009).

Several studies highlighted trends in biodiversity patterns along ecotones, but conflicting conclusions emerged (see the review of Kark, 2013). At a local scale, some authors showed that biological richness tends to peak in ecotones, whereas others argued that these areas are poorer in species (Odum, 1953; Kemp, 2000; Kark et al., 2007; Kark, 2013). At a large scale, a high dissimilarity between assemblages explained by species turnover is expected because community shifts result from replacement that rely on species-specific distribution along environmental gradients (Kark, 2013; da Silva Lima et al., 2022). In this context, estuaries represent interesting study cases as they combine a variety of ecotones (Elliott and Whitfield, 2011), longitudinal from the sea to the river, and lateral from the estuarine main channel to lateral

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habitats.

In estuarine ecosystems, abiotic factors (e.g. salinity, oxygen, turbidity, temperature) are major determinants of the spatial and temporal distributions of species (McLusky et al., 1993; Marshall and Elliott, 1998; Attrill, 2002; Guo and Pennings, 2012). Because estuaries are an interface between the sea and the river, the estuarine fish assemblages are likely to be composed of marine, freshwater, diadromous and even resident species (Potter et al., 2015; Whitfield et al., 2022). The pattern of species diversity (α -diversity) in estuaries has been described at the local scale by a conceptual model, which aims at predicting the distribution of fish species along a salinity gradient (Remane, 1934; Whitfield et al., 2012). This model suggests higher species richness at both poles of the transitional area and a decrease of richness toward brackish water (Remane, 1934). Concerning β -diversity, the pattern shows a high dissimilarity in taxonomic structure with a predominance of species turnover (Villéger et al., 2012; Barros et al., 2014; Henriques et al., 2016; da Silva Lima et al., 2022).

The responses of species to environmental gradients are often studied with classical approaches which aim at describing assemblages through the taxonomic identity of individuals (Jaureguizar et al., 2003; Barletta et al., 2005; Kolpakov and Milovankin, 2010; Nicolas et al., 2010a). However, few studies have addressed the complementarity of the functional and taxonomic approaches to disentangle the processes gouverning community assembly rule (but see Nicolas et al., 2010b; Mouillot et al., 2013; Teichert et al., 2017; Villéger et al., 2012; Henriques et al., 2016; Maciel et al., 2024). Functional ecology focuses on the description of species biological traits in communities. These attributes, which can be morphological, physiological or phenological, are assumed to reflect the influence of species on their environment (i.e. effect traits) or affect the performances of organisms (i.e. response traits) (Violle et al., 2007). Within estuaries, the prevailing stressful environmental conditions are expected to decrease functional diversity (α -diversity and β-diversity) and promote redundancy in ecological strategies (Villéger et al., 2012; Baptista et al., 2015; Dolbeth et al., 2016; Teichert et al., 2017).

Fish communities are a major biological compartment in estuarine nekton (McLusky and Elliott, 2004). As a transitional area between contrasted aquatic ecosystems, estuaries play several functional roles for numerous fish species notably thanks to the heterogeneity of environmental conditions and a diversity of habitats, including subtidal channels, mudflats or tidal marshes (Nagelkerken et al., 2015; Teichert et al., 2017; Pessanha et al., 2021). They provide migration routes for diadromous species, nursery areas for marine fishes and permanent habitat for a few resident species (McHugh, 1967; Haedrich, 1983; Elliott and Hemingway, 2008). In macrotidal systems, estuarine lateral habitats are mainly intertidal, like mudflats and marshes. These habitats are known to support essential nursery function for marine juveniles (e.g. sea bass, common sole, plaice, and mullets) (Kneib, 1997; Laffaille et al., 2001; Cattrijsse and Hampel, 2006; Day et al., 2020). Despite their important functional value, these habitats have been highly degraded by human activities during the 20th century because of harbour development or intensive land reclamation (Cattrijsse et al., 2002; Marley et al., 2020). Therefore, accessibility and connectivity of these habitats have been altered for fish communities (Bice et al., 2023). Functions of tidal and diked marshes for fish (Cattrijsse et al., 1994; Kneib, 1997; Mathieson et al., 2000; Laffaille et al., 2000, 2001; Hampel et al., 2004; Green et al., 2009) and effects of habitat restoration on fish and associated functionalities are increasingly studied (Lechêne et al., 2018; Debue et al., 2022). If the structure of fish assemblages has been widely examined longitudinally in estuaries (Jaureguizar et al., 2003; Barletta et al., 2005; Selleslagh et al., 2009; Kolpakov and Milovankin, 2010; Villéger et al., 2012; Henriques et al., 2016), the biodiversity patterns along estuarine lateral continuum has not been studied vet.

In this context, we examined community assembly rule shaping fish assemblages, more specifically diversity patterns, in three distinct habitats (estuarine main channel, tidal marsh and upper-diked marsh) of a set of lateral continuums of the Seine Estuary (NW France). The consequences of different salinity conditions on habitat-specific diversity patterns were addressed through the positions of continuums along the longitudinal estuarine gradient (polyhaline, mesohaline and mesooligohaline area). Taxonomic and functional structures of fish assemblages were investigated at two different spatial scales, i.e. α - and β -diversity. The aims of this paper are thus to (1) describe the variation of the species and ecological traits richness between habitats along lateral and longitudinal gradients, (2) investigate the levels of dissimilarity between assemblages and determine the predominant structural processes (i.e. turnover or nestedness) and (3) test the contributions of environmental and spatial factors to the variation in fish diversity.

We expected high species richness (α -diversity) in permanently flooded habitats (the estuarine main channel and diked marsh) due to their greater hydrological stability. The functional traits diversity was expected to increase in response to habitat connectivity with the marine environment and the diversity of environmental features (hydrological, trophic and structural factors). We therefore reckon on a high assemblage dissimilarity between the three habitats, with a predominance of loss of species and functional traits (nestedness process) in the case of selective colonisation by species originating from the main channel.

2. Materials and methods

2.1. Study site

The study was conducted in the Seine Estuary on the northwest coast of France (Fig. 1). This system is one of the three largest French estuaries (160 km long) and is featured by a large semidiurnal macrotidal range (average amplitude of 8.5 m). Sampling was performed close to the estuary mouth, in three areas, each area being characterized by a lateral succession from the main estuarine channel to tidal and then diked marshes. These three areas, hereafter called "sampling areas" (SA#1, SA#2, SA#3; Fig. 1), were located along a longitudinal gradient covering three salinity conditions, i.e. SA#1 was located in polyhaline waters (28,83 \pm 1,12), SA#2 in mesohaline waters (17,01 \pm 2,78), and SA#3 in meso-oligohaline waters (15,77 \pm 2,92) (Fig. 1). The main channel sampling stations (i.e. two sampling stations for SA#1 and SA#2, one sampling station for SA#3) were subtidal (Fig. 1). The tidal marsh sampling stations (i.e. three sampling stations for SA#1 and SA#3, two stations for SA#2; Fig. 1) were located in temporally flooded creeks, characterised by cyclic changes in hydrological and physicochemical parameters. Tidal marshes connected the main channel and the diked marsh. The diked marsh sampling stations (i.e. five sampling stations for SA#1 and SA#2, four sampling stations for SA#3) were featured by the presence of unsinkable dikes and hydraulic valves, which intend to regulate water fluxes within the web of man-made creeks from the diked marsh. The hydraulic network of the diked marsh is made up of canals which are supplied by rainwater and a groundwater resurgence from the alluvial plain. To retain sediment and facilitate navigation in the estuary, a sinkable dike submerged at each tide was built between the river and the tidal marsh.

2.2. Fish sampling and associated environmental parameters

Fish sampling was conducted during spring (end of May -early June) and autumn (October) during two years in the main channel and tidal marsh (2020 and 2021; sampling design is detailed in Table A1). During autumn, one supplementary sampling station was located in the top of the tidal marsh, near the unsinkable dyke (SA#1 and SA#3; Table A1). The diked marshes were sampled during spring during two years (2020 and 2021; Table A1) and autumn for one year (2020; Table A1) in five stations for SA#1 and SA#2. For technical reasons, the sampling could not be conducted during the same period in the diked marsh of SA#3. Accordingly, historical data from a fishing inventory conducted in spring 2016 in 4 stations were used as surrogates to complete the



Fig. 1. Location of the Seine Estuary (top panel, red dot) and the section of the Seine Estuary where sampling was conducted (top panel, red rectangle). The location of the three sampling areas is shown in the bottom panel by the grey area on the map (SA#1 polyhaline, SA#2 mesohaline, SA#3 meso-oligohaline). The positions of the sampling stations along the lateral continuum in the three habitats and in each sampling area are illustrated by blue dots for the main estuarine channel, green diamonds for the tidal marsh and red triangles for the diked marsh. Hydrological disruption is represented by the dotted lines indicating the position of sinkable dikes, dashed lines indicating the position of unsinkable dikes, and red crosses indicating the positions of weirs.

Table 1

Summary of the p. values of the permutation tests from the dbRDA model output for the alpha and beta diversity metrics. Complementary parameters of anova models are described in Appendix D. DistChen parameter stands for the distance of sampling site from the estuarine main channel. Significant values are highlighted in bold.

_	Salinity	Oxygen	Temperature	Elevation	DistChan	Season
Taxono	mic richness					
SA#1	0.975	0.802	0.522	0.219	0.389	0.186
SA#2	0.127	0.198	0.171	0.354	0.615	0.208
SA#3	0.099	0.446	0.915	0.273	0.649	-
Functio	onal richness					
SA#1	0.001	0.639	0.336	0.439	0.051	0.146
SA#2	0.014	0.251	0.207	0.241	0.425	0.338
SA#3	0.129	0.380	0.948	0.854	0.479	-
Taxono	mic dissimila	arity				
SA#1	0.001	0.026	0.644	0.002	0.002	0.001
SA#2	0.001	0.027	0.127	0.005	0.614	0.003
SA#3	0.001	0.011	0.081	0.083	0.445	-
Functio	onal dissimila	rity				
SA#1	0.001	0.028	0.045	0.026	0.028	0.048
SA#2	0.001	0.614	0.486	0.111	0.311	0.146
SA#3	0.001	0.024	0.045	0.053	0.515	-

dataset. Different sampling methods were used to describe the fish assemblages of the three habitats because of the heterogeneity of hydromorphologic conditions, preventing the use of similar sampling gears. Due to this sampling design, the occurrences of species were used to minimize the potential bias induced by the use of different sampling gears. Furthermore, the consistency between sampling sites was assessed by comparing the species accumulation curves made with the iNEXT package (Hsieh et al., 2016) (Figure A2). The results demonstrated an acceptable sampling completeness (>80% of species detection) for each of the three habitats (Figure A2).

The stations located in the main channel were sampled following the standardised monitoring protocol conducted for evaluating the French

transitional waters throughout EU Water Framework Directive (AFNOR, 2011). The protocol consists of several hauls across the estuary channel using a beam trawl (3 m large, 10 mm mesh size; AFNOR, 2011). Fishes from tidal marshes were sampled using a fyke net (5 mm mesh size, 20 m long and 1.60 m height) set across the main creek. The net was deployed at high water and sampling conducted during the ebb in order to catch fish leaving the creek. To cover a maximum range of marsh characteristics, stations were sampled simultaneously in each sampling area (Fig. 1, Table A1). Nets were verified every 30 min during the sampling and emptied if necessary. Sampling stopped when the water level was not high enough to cover the net inlet. Diked marshes stations were sampled using double fyke nets (5 mm mesh size). Fishing gears were positioned in a water creek for 24 h and 4 replicates were made at each sampling station for each period (Fig. 1). All fish were identified at the species level, measured to the nearest mm (fork length: FL) and released into the creeks or the main channel following measurement. The list of all identified species is mentioned in the appendix (Table E.4).

During each sampling session, the hydrological parameters (salinity, temperature -°C, and dissolved oxygen concentration – mg/L) were recorded. Moreover, spatial attributes of stations (i.e. distance from the main channel and bathymetry) were determined using a geographic information system (GIS). The distance of sampling sites from the main channel (*DistChen*, in m) was recorded by measuring the distance of the site from the nearest subtidal location. Elevation of sampling sites (*elevation*, in m) was recorded using Lidar data maps (© Shom - ROL, V20190831) in QGis© software.

2.3. Fish taxonomic and functional diversity

We described changes in fish assemblages along the lateral continuum using the taxonomic and functional facets of biodiversity. While the taxonomic facet considers all species as equally distinct, the functional facet accounts for information on species traits to determine their proximity in a multidimensional functional space (Villéger, 2008). Here the functional facet was examined by assigning species into three functional guilds, i.e. ecological traits, trophic traits and position of



Fig. 2. Changes in taxonomic richness (left panel) and functional richness (right panel) across the habitats of the estuarine lateral continuum. The coloured decomposition of boxplots within habitats represents the different sampling areas in the study site (SA#1: polyhaline area; SA#2: mesohaline area; SA#3: meso-oligohaline area).

species in the water column, which are commonly used to describe ecological niches of fish in estuaries (e.g. Henriques et al., 2017; Teichert et al., 2017; Table E4). Ecological guilds reflect the way the species use the estuary: 1) the diadromous species that use estuarine habitat as a migration corridor, 2) the estuarine species that can successfully achieve their entire life cycle in the estuary, 3) the freshwater species that sporadically use estuarine areas, 4) the marine juveniles that use the estuary as a nursery ground, and 5) the marine species that occasionally use the lower part of the estuary (Elliott et al., 2007; Table E4). The trophic guilds reflected the main food resources consumed by species and gathered six categories: 1) suprabenthic invertivorous, 2) benthic invertivorous, 3) planktivorous, 4) omnivorous, 5) herbivorous, and 6) piscivorous (Power, 1990). The distribution of fish in the water column gathered three categories: 1) benthic, 2) demersal, and 3) pelagic species (Vander Zanden and Vadeboncoeur, 2002; Table E4).

In order to estimate the range of functional traits values of the communities (functional space), we measured first the pairwise functional distances between each species using Gower's distance (Gower, 1971). Then, the outcomes were synthesised into multidimensional functional space by applying PCoa (Principal Co-ordinate analysis) on the distance matrix. The first three axes of the PCoa were selected using the highest *mSD* value from *quality_funct_space* function, which provides quantitative metrics for the quality of the functional space (Maire et al., 2015).

Diversity was investigated at both local scale (α -diversity) and sampling area scale (i.e., between sampling stations, that corresponds to pairwise β -diversity) to disentangle processes shaping fish assemblages along the lateral estuarine continuum. For each diversity facet, we used species presence/absence data (Table E4). Accordingly, α -diversity was examined for each sampling station using taxonomic and functional richness, which did not account for species abundance. The taxonomic richness was defined as the total number of species observed in a station during a given sampling session. The functional richness reflects the diversity of ecological guilds in the assemblage and was assessed by calculating the volume of the functional space filled by the species (Villéger, 2008) with the dbFD function of the FD package (Laliberté and Legendre, 2010). The β -diversity was assessed by the Sørensen index calculated on presence/absence data. This total dissimilarity (β-diversity) was then partitioned into two components according to the framework proposed by Baselga (2010). The turnover of species/traits between two communities was measured using the Simpson dissimilarity index, while the nestedness component (species loss/gain) was measured with the Sørensen nestedness component index (Baselga, 2012). For each sampling area, the β -diversity value was calculated between each pair of sampling stations within season (spring and autumn) and year using the beta.pair (for taxonomic dissimilarity) and

functional.beta.pair (for functional dissimilarity) functions, as implemented in the *betapart* package (Baselga, 2012).

2.4. Statistical analysis

2.4.1. Lateral patterns of fish diversity

First, we investigated changes in taxonomic and functional richness along the lateral continuum using General Linear Models (GLMs). For each diversity facet, a model was adjusted to examine the effects of pairs of habitat-sampling area, their interaction (habitat*sampling area) and season (spring and autumn). GLM models were built using glm function and the significance levels of parameters were assessed using an ANOVA test based on a Chi-square statistic. Finally, a post-hoc test was performed between each pair of significant descriptor levels using the TuckeyHSD function. In a second step, we used Linear Mixed Models (LMMs) to test for the effects of lateral habitats on the taxonomic and functional β-diversity values between pairs of habitat stations (main channel - tidal marsh and tidal marsh - dyked marsh). For each diversity facet and β -diversity component, we adjusted a LMM model with the pair of habitat-sampling area, interaction of habitat*sampling area and season as fixed effects. To prevent non-independency of data when comparing paired stations, models were implemented with the station as a random effect (Row et al., 2017). The LMMs were built using the lme function of the 'lme4' package (Bates et al., 2015). When the data did not meet the assumptions of normality and variance homogeneity, non-parametric framework based on permutation tests were used on the mixed linear model to study the significance of differences between groups. Permutation tests were made on lme object with the PermTest function of the 'pgrimess' package (Giraudoux et al., 2023).

2.4.2. Environmental and spatial drivers of fish diversity

Collinearity between environmental descriptors is a common feature of ecotone ecosystems. Accordingly, we firstly assessed the correlation between variables using the Spearman tests to measure the degree of information redundancy. The correlation tests revealed some correlations between descriptors along the main channel-marsh continuum (Figure A3). Accordingly, we used a variation partitioning procedure to determine the unique and shared contributions of environmental and spatial sets of predictors to explain variation in β -diversity values (Borcard et al., 1992). For each diversity metric, we conducted a partial redundancy analysis with the *varpart* function of the *vegan* package (Oksanen et al., 2015) to determine the relative influence of environmental (i.e. salinity, oxygen, temperature), spatial (DistChen and elevation) and temporal (season - spring and autumn) processes. The proportion of explained variance was assessed through the ajdR² statistic. The significance levels were assessed using permutation tests on



Fig. 3. Taxonomic (top panel) and functional (bottom panel) dissimilarity in community composition between the two pairs of studied habitats along the estuarine lateral continuum (Main channel/Tidal marsh; Tidal marsh/Diked marsh). The total dissimilarity (Total) is partitioned into two components: species turnover between communities (Turn) and nestedness between communities (Nest). The coloured decomposition of boxplots within habitats represents the different sampling areas in the study site (SA#1: polyhaline area; SA#2: mesohaline area; SA# 3: meso-oligohaline area).

the RDA model built with *dbRDA* function. The effect sizes of environmental, spatial and seasonal descriptors were represented by the coefficient of each descriptor to the dbRDA axes (Tables D.3 and D.4).

2.4.3. Lateral distribution of functional guilds

To support our findings on fish functional structure, we used GLM models to examine the fluctuations in occurrence of the three functional guilds along the lateral continuum for the three sampling areas. For each functional group, a logistic GLM model was built to test for the effect of habitat type, sampling area, interaction habitat*sampling area and season on the group occurrence (i.e. presence/absence). The significance levels were assessed using ANOVA tests based on the Chi-square statistic. Finally, we predicted occurrence probabilities of fish functional groups along the lateral gradients for the three sampling areas by applying *predict.glm* function. The occurrence probabilities between habitats were illustrated by heatmaps drawn with the 'ggplot' package.

All analyses were implemented in R (R Core Team, 2021) within the integrated development environment (IDE) R-studio.

3. Results

3.1. Taxonomic and functional alpha diversities

Overall, the taxonomic richness exhibited a concave shape curve in SA#1 and SA#2, where higher richness values were recorded at the margin of the lateral continuum (i.e. main channel and diked marshes; Fig. 2). In contrast, the taxonomic richness appeared more balanced in SA#3. The species richness was on average higher in the diked marshes (i.e. until 30 species) in comparison to the two other habitats (ANOVA, P < 0.001; Fig. 2; Table B1). The interactive effect between habitat type and sampling area on the taxonomic richness was significant (ANOVA, P < 0.001), which suggests different species repartition patterns depending on the sampling area. In SA#2, the minimum species richness was observed in the tidal marsh, while the maximum values were reported for the diked marsh (TukeyHSD, P < 0.001; Fig. 2; Table B.2). In the diked marshes, the taxonomic richness increased in SA#2 (TukeyHSD, P < 0.001; Fig. 2).

In contrast to the taxonomic richness, the functional richness decreased toward the high part of the lateral continuum (Fig. 2), being significantly lower in the diked marshes in comparison to the tidal

marshes and main channel (ANOVA, P < 0.001; Table B1). Within the sampling areas, the functional richness was lower in the diked marsh of SA#1 (TukeyHSD, P < 0.01; Table B2) and in the tidal marsh of SA#2 (TukeyHSD, P < 0.03; Table B2) in comparison to the other habitats of the lateral continuum (Fig. 2).

3.2. Taxonomic and functional beta diversities

The total taxonomic dissimilarity ranged between low (0.13) and high (1.00) values, with the highest pairwise values reported between main channel and tidal marsh habitats (LMM, P < 0.001; Fig. 3; Table C1). The dissimilarity partitioning revealed that species turnover was lower between the tidal marshes and the diked marshes than between the tidal marshes and the main channel (LMM, P < 0.001; Fig. 3; Table C3). In contrast, the contribution of turnover and nestedness between tidal marshes and diked marshes differed between the sampling areas (turnover: LMM, P < 0.001; nestedness: LMM, P < 0.012; Table C2). In SA#2, the nestedness (Nest) component was the main driver of taxonomic β -diversity (LMM, P < 0.03; Table C3), whereas the contribution of turnover was dominant in the two other areas. The nestedness component of taxonomic β -diversity fluctuated seasonally (LMM, P < 0.001; Table C2), with higher species nestedness in autumn.

The total functional β -diversity revealed high dissimilarity in functional traits along the lateral continuum (total β -diversity >0.60), but values did not differ between the two pairs of habitats (LMM, P < 0.08; Fig. 3; Table C1). The turnover and nestedness processes were equivalent between the two pairs of habitats (Turnover: LMM, P = 0.8; Nestedness: P = 0.4; Table C2). On the contrary, comparison among sampling areas revealed that the turnover component was lower between tidal and diked marshes in SA#2 and SA#3 (LMM, P = 0.04; LMM, P = 0.002; Table C3).

3.3. Environmental and spatial drivers of fish diversity

The percentages of variance in taxonomic and functional diversity explained by the partial RDAs ranged from 7 % to 64 % depending on the diversity metric and sampling area (Fig. 4). For most of the diversity metrics, the results emphasized that a large proportion of variation was explained by the shared effect of environmental and spatial descriptors (Environmental \bigcirc Spatial; Fig. 4). For the taxonomic richness, the



Fig. 4. Effects of environmental, spatial, temporal and shared parts of environmental and spatial descriptors in the variation of the diversity facets. The values of bar plots illustrate the proportion of the explained variance (R²adj) by each group of descriptors for the taxonomic and functional diversity in the studied area (SA#1: polyhaline area; SA#2: mesohaline area; SA#3: meso-oligohaline area).

variance explained by the model remained low (between 7 and 18 %) and the effects of descriptors was not significant (Fig. 4; Table D1). For the functional richness, the greatest proportion of explained variation (between 12 and 46 %) was attributable to the shared contribution of the environmental and spatial descriptors, especially in SA#1 (SA#1: 46 %; Fig. 4). The functional richness was significantly affected by salinity changes in SA#1 and SA#2 (Fig. 4; Table 1; Table D1).

For the taxonomic dissimilarity, the explained deviance ranged from 60 to 65 % (Fig. 4), with a large fraction attributable to the shared contribution of the environmental and spatial descriptors (SA#1 = 54 %, SA#2 = 51 % and SA#3 = 52 % of explained variance). Significant effects of salinity and oxygen were highlighted for the three sampling

areas (Table 1; Table D2). In addition, a significant effect of the elevation was identified for SA#1 and SA#2, whereas the distance from the main channel was only significant for SA#1 (Table 1; Table D2). Lastly, the results illustrated the significant seasonal effect on the variation of taxonomic dissimilarity for SA#1 and SA#2 (Table 1; Table D2).

For the functional dissimilarity, the partial RDAs explained a greater proportion of statistical deviance in SA#1 (43 % of explained deviance; Fig. 4). The largest fraction of functional dissimilarity was explained by the shared part of environmental and spatial descriptors for the three sampling areas (SA#1: 29 %, SA#2: 10%, SA#3: 17% explained variation). The functional dissimilarity was significantly affected by salinity for the three sampling areas, and by oxygen and temperature for SA#1



Fig. 5. Lateral distribution of the ecological, trophic and position guilds. The distributions of the functional guilds are illustrated by the colour gradients and represent the probability of a guild occurring in each habitat of the sampling areas.

and SA#2 (Table 1; Table D2). The results illustrated significant effects of elevation, distance from main channel and season for SA#1 only (Table 1; Table D2).

3.4. Guilds distribution along the lateral continuum

The lateral distribution of ecological guilds revealed a similar occurrence pattern regardless of the sampling area considered (Fig. 5, Table E1). Overall, the occurrence of diadromous species remained stable between habitats (ANOVA, P = 0.3). In contrast, the occurrence of the estuarine species (ANOVA, P < 0.001) and freshwater species (ANOVA, P < 0.001) increased along the lateral continuum, whereas the occurrence of marine juveniles decreased (ANOVA, P < 0.001).

The occurrences of benthic (ANOVA, P = 0.09) and suprabenthic invertivorous (ANOVA, P = 0.07) were comparable between habitats (Fig. 5, Table E2). Planktivorous fish (ANOVA, P < 0.001) declined along the lateral continuum, while the occurrences of herbivorous (ANOVA, P < 0.001) and omnivorous (ANOVA, P < 0.001) increased (Fig. 5, Table E2). The piscivorous fish appeared mainly associated with the diked marshes (ANOVA, P = 0.01; Table E2). In the main channel and tidal marshes, the occurrence of omnivorous fish surged toward SA#3 (ANOVA, P = 0.001; Table E2). In the diked marshes, the occurrence of herbivorous fish increased toward SA#3 (ANOVA, P = 0.02; Table E2).

For the water column occupancy, the occurrences of benthic species were stable along the lateral continuum (ANOVA, P = 0.09; Table E3). On the contrary, demersal species increased along the lateral habitats (tidal and diked marsh) (ANOVA, P = 0.02; Table E3). Finally, the occurrence of pelagic species increased in the three habitats towards SA#3 (ANOVA, P = 0.001; Table E3).

4. Discussion

Species diversity patterns along estuarine ecotones are described by several conceptual models, which illustrate species distribution along the multiple environmental gradients that shape these ecosystems, including salinity (Whitfield et al., 2012; Basset et al., 2013; Maciel et al., 2024). Although previous studies investigated the effects of estuarine ecotones on fish assemblages from the sea to upstream main channel waters (Jaureguizar et al., 2003; Barletta et al., 2005; Selleslagh et al., 2009; Kolpakov and Milovankin, 2010; Villéger et al., 2012; Henriques et al., 2016), diversity patterns along lateral gradients were never addressed before. In this context, our study describes how the taxonomic and functional structures of fish assemblages are structured from the main channel to the upper part of the lateral habitats. In this purpose, we had to combine datasets produced from different protocols because of the heterogeneity of hydro-morphologic conditions and associated diverse sampling conditions along the lateral estuarine ecotones. While the main channel was sampled by an active method (beam trawl), the tidal and diked marshes were sampled using passive fishing gears (fyke nets). Species occurrences were thus used instead of species abundance in statistical analyses in order to minimize the potential biases. However, the use of different sampling gears may influence the species observed due to the selectivity of some methods. For example, the species richness in the main channel is probably underestimated because beam trawl mainly focuses on benthic and demersal species, while pelagic species are irregularly caught when raising the trawl. Nevertheless, the species accumulation curves demonstrated an acceptable sampling completeness (>80% of species detection) for each of the three habitats and for the two sampling methods (Figure A2). These limitations should, however, be kept in mind when interpreting the results. Our findings demonstrate that the succession of lateral habitats strongly structures the taxonomic and functional fish assemblages. Interestingly, the concave shape of taxonomic richness in lateral ecotones was comparable to the longitudinal fish diversity shape occurring between marine and freshwater areas at the estuarine scale

(Whitfield et al., 2012). This diversity pattern was characterized by high species richness in the habitats located on the poles of the ecotone (main channel and diked marshes) and globally low species number in the transitional areas (tidal marshes). The high taxonomic β-dissimilarity between the main channel and tidal marsh, driven by the turnover component, revealed the important changes in species composition between subtidal and intertidal habitats (Leprieur et al., 2009). Despite a high hydrological connectivity, the constraints of environmental factors probably act as ecological boundaries for several fish species inhabiting the main channel (e.g. brill, tub gurnard, lesser weever, bib) and lead to the replacement of strict marine species by freshwater species. Such a process is expected to occur in ecotonal areas where shifts in abiotic factors determine species distribution (Walker et al., 2003; Villéger et al., 2012; Kark, 2013; Barros et al., 2014; Teichert et al., 2017). In contrast, turnover was lower between tidal marsh and diked marsh assemblages. These habitats shared more species (bream, carp, rudd, sand smelt) and nested assemblages seem to occur on lateral habitats. Nestedness is expected to reflect several ecological mechanisms such as local extinction, selective colonisation, and species loss related to their environmental tolerance (Ulrich et al., 2009; Leprieur et al., 2009). On the lateral areas, nestedness illustrates the decline of local species richness from diked marshes to tidal marshes, which can be explained by the constraint of several environmental factors, including recurrent emersion and huge variability of local conditions (e.g. salinity, oxygen or temperature).

The functional facets (α - and β -diversity) of the fish assemblages showed a contrasting pattern. The decline of local richness and the high dissimilarity of ecological traits between habitats suggested that niche filtering processes occur along the lateral ecotones (Bernard-Verdier et al., 2012; Villéger et al., 2012; Kraft et al., 2015; Teichert et al., 2017). Indeed, our results highlighted important changes in the occurrence of functional guilds. Marine juveniles and planktivorous species decreased along the lateral continuum, whereas freshwater and herbivorous species were promoted by the decline of salinity. Moreover, only a few diadromous, estuarine and marine juvenile species with omnivorous species from the main channel seem to be able to colonize the lateral habitats. These observations might be explained by the homogenisation of environmental conditions (e.g. salinity, turbidity, elevation, substrate type) and the decreasing prey diversity, which results in a reduction of available ecological niches toward diked marshes (Macarthur and Levins, 1967; Kraft et al., 2015; Dolbeth et al., 2016, Moreno-Valcárcel et al., 2016; Day et al., 2020).

The diversity patterns of fish assemblages differed according to the sampling areas, for each habitat, probably in response to changes in salinity conditions. Similar findings were already reported in tropical estuaries, where differences in species and trait composition between habitats are influenced by water salinity and transparency (Maciel et al., 2024). In the main channel stations, the taxonomic and functional richness increased toward the estuary mouth, which was consistent with the rising proportion of marine species in assemblages within polyhaline areas (Whitfield et al., 2012). In contrast, fish assemblages of lateral habitats showed an opposite trend, which could be explained by the coexistence of several functional guilds (i.e. freshwater, marine juvenile, diadromous, estuarine). In the meso-oligohaline area (SA#2 and SA#3), the lateral habitats provide foraging and refuge areas for marine juvenile, estuarine and diadromous species (e.g. sea bass, sprat, sand goby, thinlip mullet or flounder) and also constitute important shelter from the high salinity and current velocity at high tide for the freshwater species. In addition, community assembly rules between tidal and diked marshes were mainly explained by nestedness processes. It is likely that the ubiquitous species (marine juvenile, estuarine and freshwater species) that use the tidal marshes were able to colonize the diked marshes, where assemblages are composed of a high proportion of resident freshwater and diadromous species with omnivorous trophic strategies. Elsewhere, freshwater and diadromous species from diked marshes may also disperse in the tidal marshes where and when the hydraulic

connectivity between the two habitats is made possible. The hydraulic connectivity and dispersal possibility are known to influence fish diversity (Villéger, 2008; Peláez and Pavanelli, 2019). In the present case, the diked marshes could play the role of favourable habitats in estuaries for freshwater and diadromous species, like European eel, by impounding low salinity water. As a transitional habitat, the tidal marshes can be considered as steppingstones by temporarily connecting functional patches in estuarine landscape during the estuarine migration of diadromous, marine and freshwater juveniles (Saura et al., 2014). Furthermore, a seasonal pattern in community assembly was revealed for lateral habitats (SA#2 and SA#3). In these habitats, the results illustrated lower taxonomic and functional nestedness during the spring period. This trend probably reflects the seasonal behaviour of some fish species, such as European flounder, three-spined stickleback or topmouth gudgeon, that mainly use the tidal marsh during spring as a foraging ground (Hampel et al., 2004; Green et al., 2009).

Our results highlighted contrasting community assembly rules between sampling areas, which can be linked to different environmental filters and potential connectivity alteration across lateral habitats (Villéger, 2008). Indeed, the high functional turnover between tidal and diked marshes in the polyhaline area (SA#1) could reflect different ecological functioning or dispersal limitations for fish (Leprieur et al., 2009; Villéger et al., 2010). This can result from poor lateral connectivity of the diked marsh in this area (Leprieur et al., 2009; Villéger et al., 2010; Liu and Wang, 2018; Peláez and Pavanelli, 2019). The intensification of human activity in the Seine Estuary, associated to harbour extension or land reclamation, has led to a major fragmentation and loss (over 70 %) of highly valuable habitats for fish in the estuarine floodplain (Lesueur and Lesourd, 1999; Le Pape et al., 2007; Rochette et al., 2010). Consequently, a great proportion of the estuarine lateral connectivity was impacted. This resulted in the isolation of subtidal refuges at low tide that became relatively distant from the tidal zone and diked marshes. The proximity and structure of these areas are known to determine the extent and frequency of lateral habitat utilization by fish and productivity of intertidal areas (Allen et al., 2007; Kneib, 2003; Le Pichon et al., 2017; Teichert et al., 2018; Bice et al., 2023). Finally, the presence of several dams and hydraulic infrastructures between tidal and diked marshes seems to restrain further the lateral connectedness between tidal and diked marshes.

To conclude, the consideration of the lateral ecotones appears as a crucial component for the understanding of fish diversity and associated ecological functions in estuarine habitats. Our study investigating three habitats along the longitudinal salinity gradient supports the importance of connectivity between the main channel and estuarine marshes for sustaining a high level of taxonomic and functional diversity in fish assemblages. The functional relationships among these habitats appear essential for freshwater fish survival, but also for euryhaline,

Appendix A

Table A.1

diadromous and resident species. Among the multiple fish species generally found in the main channels of estuaries, some will need to migrate laterally during their estuarine life cycle (seabass, sand goby, thinlip mullet, flounder, European eel, bream, etc.). In addition, the consideration of different sampling areas shows that variations in diversity patterns exist along the longitudinal gradient. There are therefore several lateral ecotones with distinct but complementary ecological functions for estuarine fish communities, depending on their position along the salinity gradient. For this reason, the conservation of lateral landscapes and its connectivity with other estuarine areas (particularly the main channel) should be prioritised in management policies and restoration plans, especially in meso-oligohaline areas and diked marshes, which constitute a unique component of the estuarine habitat mosaic.

CRediT authorship contribution statement

Matia Pavkovic: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. Alexandre Carpentier: Writing – original draft, Validation, Supervision, Methodology, Investigation, Conceptualization. Sylvain Duhamel: Validation, Methodology, Investigation, Conceptualization. Laure Carassou: Writing – original draft, Validation. Jérémy Lobry: Writing – original draft, Validation. Eric Feunteun: Writing – original draft, Validation. Nils Teichert: Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Summary of the sampling effort in each habitat of the study site. The number of sampling stations is described for the three habitats (main channel, tidal marsh and diked marsh) within each of three sampling areas (SA#1, SA#2, SA#3) for the two studied years. The number of replicates per sampling station is mentioned in parentheses. See Fig. 1 for sampling area locations.

		Spring	Spring			Autumn	
Habitat	Sampling Area	2016	2020	2021	2020	2021	
Main channel	SA#1		2 (1)	2 (1)	2 (1)	2 (1)	
	SA#2		2 (2&1)	2 (2&1)	2 (2&1)	2 (2&1)	
	SA#3		1 (2)	1 (2)	1 (2)	1 (2)	
Tidal marsh	SA#1		2 (4)	3 (4)	2 (4)	3 (4)	
	SA#2		2 (4)	2 (4)	2 (4)	2 (4)	
					<i>,</i> ,		

Table A.1 (continued)

		Spring	Spring			Autumn		
Habitat	Sampling Area	2016	2020	2021	2020	2021		
	SA#3		2 (4)	3 (4)	2 (4)	3 (4)		
Diked marsh	SA#1		5 (4)	5 (4)	5 (4)			
	SA#2		5 (4)	5 (4)	5 (4)			
	SA#3	4 (4)	1 (5)	1 (5)				



Fig. A.2. Species accumulation curves made for the three studied habitats for the two seasons (Main channel = 28, Tidal marsh = 27, Diked marsh = 35).



Fig. A.3. Correlation plot between the physico-chemical and spatial descriptors.

Appendix B

Table B.1

Summary of the ANOVA model output for the taxonomic and functional richness. Here, 'sampling areas' (SA#1, SA#2, SA#3) refer to positions along the longitudinal gradient, while 'habitat' refers to either the main channel, or the tidal and diked marshes.

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Taxonomic richness						
Habitat	2	107.6	53.81	7.692	< 0.001	***
Sampling areas	2	32.4	16.22	2.319	0.104	
					(continued	on next page)

Table B.1 (continued)

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Season Habitat X Sampling areas Functional richness	2 4	33.6 154.7	16.80 38.67	2.402 5.528	0.096 <0.001	***
Habitat Sampling areas	2 2 2	0.290252 0.008231 0.010474	96 94 93	0.91958 0.91135 0.90087	<0.001 0.630 0.555	***
Habitat X Sampling areas	4	0.116082	92 88	0.78479	0.055	*

Table B.2

Summary of the TuckeyHSD post-test output for the taxonomic and functional richness.

	diff	lwr	upr	p adj	
Taxonomic richness					
Tidal marsh - Main channel	-0.0515873	-1.7154950	1.612320	0.996	
Diked marsh - Main channel	2.0595238	0.5746657	3.544382	0.003	**
Diked marsh - Tidal marsh	2.1111111	0.6093982	3.612824	0.003	**
Diked marsh X SA#2 - Dicked marsh X SA#1	3.3011432	0.6980293	5.9042570	0.003	**
Diked marsh X SA#2 - Main channel X SA#2	4.0193517	1.0135347	7.0251687	0.001	**
Diked marsh X SA#2 - Tidal marsh X SA#2	5.0656414	1.6220454	8.5092374	< 0.001	***
Functional richness					
Tidal marsh - Main channel	-0.0515873	-1.7917263	1.688552	0.997	
Diked marsh - Main channel	2.0595238	0.5066375	3.612410	0.006	**
Diked marsh - Tidal marsh	2.1111111	0.5405979	3.681624	0.005	**
Diked marsh X SA#1 - Main channel X SA#1	-0.21900738	-0 34402064	-0.09399411	<0.001	**
Tidal marsh X SA#2 - Main channel X SA#2	-0.14985380	-0.28871232	-0.01099527	0.024	*

Appendix C

Table C.1

Summary of the LMM outputs for the taxonomic and functional dissimilarity. "hab" is habitat, "samp.area" is sampling area.

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Taxonomic dissimilarity							
Pairs.hab	0.63967	0.63967	1	46.796	78.007	< 0.001	***
Pairs.samp area	0.02813	0.01406	2	28.582	1.715	0.197	
Pairs.season	0.02584	0.02584	1	29.273	3.151	0.086	
Pairs.hab X Pairs.samp area	0.02877	0.01438	2	47.019	1.754	0.184	
Functional dissimilarity							
Pairs.hab	0.123945	0.123945	1	39.360	3.1806	0.082	
Pairs.samp area	0.018758	0.009379	2	17.430	0.2407	0.788	
Pairs.season	0.008658	0.008658	1	22.311	0.2222	0.641	
Pairs.hab X Pairs.samp area	0.183604	0.091802	2	39.936	2.3557	0.107	

Table C.2

Summary of the permutation test outputs for the taxonomic and functional dissimilarity. "hab" is habitat, "samp.area" is sampling area.

	P value	
Taxonomic turnover		
Pairs.hab	<0,001	***
Pairs.samp area	0,089	
Pairs.season	0,37	
Pairs.hab X Pairs.samp area	0,002	**
Taxonomic nestedness		
Pairs.hab	0,012	*
Pairs.samp area	0,064	
Pairs.season	<0,001	***
Pairs.hab X Pairs.samp area	<0,001	***
Functional turnover		
Pairs.hab	0,8	

Table C.2 (continued)

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	P value	
Pairs.samp area	0,7	
Pairs.season	0,6	
Pairs.hab X Pairs.samp area	<0,001	***
Functional nestedness		
Pairs.hab	0,4	
Pairs.samp area	0,72	
Pairs.season	0,33	
Pairs.hab X Pairs.samp area	0,35	

Table C.3

Summary of size effects for the taxonomic and functional facets of dissimilarity.

	Estimate	Std. Error	df	t value	$\Pr(> t)$	
Taxonomic turnover						
Tidal marsh - Diked marsh	-0.24795	0.07860	51.34882	-3.155	0.002	**
Tidal marsh - Diked marsh X SA#2	-0.24430	0.10256	50.63244	-2.382	0.021	*
Taxonomic nestedness						
Spring	-0.07254	0.03419	42.66584	-2.122	0.039	*
Tidal marsh - Diked marsh X SA#2	0.13698	0.06347	49.74594	2.158	0.035	*
Functional turnover						
Tidal marsh - Diked marsh X SA#2	-0.176567	0.085425	43.479152	-2.067	0.044	*
Tidal marsh - Diked marsh X SA#3	-0.331671	0.103255	41.860364	-3.212	0.002	**

Appendix D

Table D.1

Summary of the permutation test from the dbRDA model outputs for the alpha diversity matrix.

	Descriptor	Df	SumOfSqs	F	Pr(>F)	
Taxonomic richne	ess					
SA#1	Salinity	1	0.0003	0.0014	0.975	
	Oxygen	1	0.0115	0.0508	0.802	
	Season	1	0.3865	1.7094	0.186	
	Temperature	1	0.0825	0.3649	0.522	
	Elevation	1	0.3469	1.5344	0.219	
	DistChen	1	0.1693	0.7488	0.389	
SA#2	Salinity	1	1.1486	2.7576	0.127	
	Oxygen	1	0.7716	1.8525	0.198	
	Season	1	0.6515	1.5641	0.208	
	Temperature	1	0.7743	1.8589	0.171	
	Elevation	1	0.4464	1.0717	0.354	
	DistChen	1	0.1035	0.2485	0.615	
SA#3	Salinity	1	1.0755	3.2854	0.099	
	Oxygen	1	0.2087	0.6375	0.446	
	Temperature	1	0.0033	0.0100	0.915	
	Elevation	1	0.4917	1.5020	0.273	
	DistChen	1	0.0785	0.2399	0.649	
Fonctional richn	ess					
SA#1	Salinity	1	0.214074	26.7494	0.001	***
	Oxygen	1	0.002253	0.2815	0.639	
	Season	1	0.009396	1.1740	0.336	
	Temperature	1	0.017807	2.2250	0.146	
	Elevation	1	0.005398	0.6745	0.439	
	DistChen	1	0.035157	4.3930	0.051	<u>. </u>
SA#2	Salinity	1	0.075079	7.7493	0.014	*
	Oxygen	1	0.015926	1.6438	0.251	
	Season	1	0.016907	1.7451	0.207	
	Temperature	1	0.009362	0.9663	0.338	
	Elevation	1	0.013500	1.3934	0.241	
	DistChen	1	0.006318	0.6521	0.425	
SA#3	Salinity	1	0.028633	2.6655	0.129	
	Oxygen	1	0.008897	0.8283	0.380	
	Temperature	1	0.000046	0.0042	0.948	

Table D.1 (continued)

Descriptor	Df	SumOfSqs	F	Pr(>F)	
Elevation	1	0.000404	0.0377	0.854	
DistChen	1	0.007649	0.7120	0.479	

Table D.2		
Summary of the permutation test fr	om the dbRDA model outputs for	the beta diversity matrix.

	Descriptor	Df	SumOfSqs	F	Pr(>F)	
Taxonomic dissi	milarity					
SA#1	Salinity	1	2.15048	34.8359	0.001	**
	Oxygen	1	0.22015	3.5663	0.026	*
	Season	1	0.03658	0.5925	0.644	
	Temperature	1	0.64486	10.4462	0.001	**
	Elevation	1	0.42915	6.9519	0.002	**
	DistChen	1	0.30706	4.9741	0.002	**
SA#2	Salinity	1	2.71532	27.2912	0.001	**
	Oxygen	1	0.29918	3.0070	0.027	*
	Season	1	0.64510	6.4838	0.003	**
	Temperature	1	0.17533	1.7622	0.127	
	Elevation	1	0.55799	5.6083	0.005	**
	DistChen	1	0.06703	0.6738	0.614	
SA#3	Salinity	1	2.08549	25.2099	0.001	**
	Oxygen	1	0.38714	4.6798	0.011	*
	Temperature	1	0.20149	2.4357	0.081	
	Elevation	1	0.19630	2.3730	0.083	
	DistChen	1	0.07485	0.9048	0.445	
Fonctional diss	imilarity					
SA#1	Salinity	1	1.90355	14.1325	0.001	**
	Oxygen	1	0.37043	2.7502	0.028	*
	Season	1	0.35615	2.6441	0.048	*
	Temperature	1	0.32690	2.4270	0.045	*
	Elevation	1	0.46823	3.4763	0.026	*
	DistChen	1	0.42668	3.1678	0.028	*
SA#2	Salinity	1	0.9447	4.9029	0.001	***
	Oxvgen	1	0.1352	0.7017	0.614	
	Season	1	0.3102	1.6100	0.146	
	Temperature	1	0.1714	0.8895	0.486	
	Elevation	1	0.3402	1.7654	0.111	
	DistChen	1	0.2241	1.1630	0.311	
SA#3	Salinity	1	1.12613	6.2785	0.001	***
	Oxygen	1	0.44342	2.4722	0.024	*
	Temperature	1	0.38593	2.1517	0.045	*
	Elevation	1	0.40439	2.2546	0.053	
	DistChen	1	0 16278	0.0075	0.515	

Table D.3

Summary of size effect of descriptors on the alpha diversity metrics. The size effects are described by the coefficients of the descriptor on the dbRda axes.

	Descriptor	dbRDA1
Taxonomic richi	ness	
SA#1	Salinity	0.0405
	Oxygen	0.0069
	Temperature	0.0223
	Season	-0.0237
	Elevation	0.0341
	DistChen	0.0001
SA#2	Salinity	-0.0353
	Oxygen	0.0260
	Temperature	0.0261
	Season	-0.1763
	Elevation	-0.0810
	DistChen	0.0001

	Descriptor	dbRDA1
SA#3	Salinity	-0.0137
	Oxygen	0.0052
	Temperature	0.0082
	Elevation	-0.0580
	DistChen	0.0001
Functional rich	ness	
SA#1	Salinity	0.0010
	Oxygen	0.0106
	Temperature	0.0098
	Season	-0.0178
	Elevation	-0.0327
	DistChen	0.0001
SA#2	Salinity	0.0083
	Oxygen	-0.0267
	Temperature	-0.0646
	Season	0.0976
	Elevation	0.0081
	DistChen	-0.0001
SA#3	Salinity	-0.0196
	Oxygen	0.0588
	Temperature	0.0197
	Elevation	-0.0164
	DistChen	0.0002

Table D.4

Summary of size effect of descriptors on the beta diversity metrics. The size effects are described by the coefficients of the descriptor on the dbRda axes.

Taxonomic dissimilarity Control Control SA#1 Salinity 0.0054 -0.0055 Oxygen 0.0018 -0.0011 Temperature -0.0006 -0.0056 Season 0.0705 0.1298 Elevation -0.0185 -0.1719 Oxygen -0.0024 -0.0065 Same 0.0497 0.3175 Elevation -0.0177 -0.0046 Oxygen -0.0024 -0.0045 Season 0.0497 0.3175 Elevation -0.177 -0.0046 DistChen -0.0091 0.0511 Oxygen -0.0214 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0219 0.0316 0.0211 DistChen -0.0004 -0.0003 -0.0003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 - Temperature 0.0047 -0.01042078 <th></th> <th>Descriptor</th> <th>dbRDA1</th> <th>dbRDA2</th>		Descriptor	dbRDA1	dbRDA2
$\begin{array}{c cccccc} \text{Asymmetry} & \text{Salinity} & 0.0054 & -0.0055 \\ \text{Oxygen} & 0.0018 & -0.0011 \\ \text{Temperature} & -0.0006 & -0.0055 \\ \text{Season} & 0.0705 & 0.1298 \\ \text{Elevation} & -0.0185 & -0.1719 \\ \hline & \text{DistChen} & -0.0004 & 0.0002 \\ \hline & \text{SA\#2} & \text{Salinity} & -0.0011 & 0.0090 \\ \text{Oxygen} & -0.0024 & -0.0065 \\ \text{Temperature} & -0.0059 & 0.0045 \\ \text{Season} & 0.0497 & 0.3175 \\ \text{Elevation} & -0.0177 & -0.0046 \\ \hline & \text{DistChen} & -0.0007 & 0.00008 \\ \hline & \text{SA#3} & \text{Salinity} & 0.0091 & 0.0511 \\ \text{Oxygen} & -0.0291 & 0.2020 \\ \text{Temperature} & -0.0054 & 0.0251 \\ \text{Elevation} & -0.0291 & 0.2020 \\ \hline & \text{Temperature} & -0.00044 & -0.00008 \\ \hline & \text{SA#3} & \text{Salinity} & 0.0091 & 0.05111 \\ \hline & \text{Oxygen} & -0.0291 & 0.2020 \\ \hline & \text{Temperature} & -0.0054 & 0.0251 \\ \text{Elevation} & -0.0004 & -0.00003 \\ \hline & \text{SA#41} & \text{Salinity} & -0.0059 & -0.0307 \\ \hline & \text{Oxygen} & 0.0188 & 0.0255 \\ \text{Temperature} & 0.0047 & -0.01042078 \\ \text{Season} & 0.0134 & 0.0696 \\ \text{Elevation} & -0.0001 & 0.00002 \\ \hline & \text{SA#2} & \text{Salinity} & -0.0024 & -0.0137 \\ \hline & \text{Oxygen} & -0.0137 & 0.0158 \\ \text{Temperature} & 0.0047 & -0.01042078 \\ \text{Season} & 0.0134 & 0.0696 \\ \text{Elevation} & -0.0026 & -0.0307 \\ \hline & \text{Oxygen} & -0.0137 & 0.0158 \\ \text{Temperature} & -0.0026 & 0.0608 \\ \text{Season} & -0.0137 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.0011 & 0.0005 \\ \hline & \text{SA#3} & \text{Salinity} & 0.0019 & 0.1038 \\ \hline & \text{Oxygen} & -0.0037 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.00137 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.00137 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.00137 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.00137 & 0.0158 \\ \text{Temperature} & -0.00276 & 0.0608 \\ \text{Season} & -0.0137 & 0.0158 \\ \text{Temperature} & -0.0276 & 0.0608 \\ \text{Season} & -0.0616 & -0.0806 \\ \text{Elevation} & -0.0024 & -0.1709 \\ \text{Oxygen} & -0.0137 & 0.0158 \\ \text{Temperature} & -0.0276 & 0.0608 \\ \text{Season} & -0.0616 & -0.0806 \\ \text{Elevation} & -0.0027 & 0.0823 \\ \text{Oxygen} & -0.0127 & 0.0823 \\ \text{Oxygen} $	Townsenis dissin-11			
$ \begin{array}{c cccccc} SA \# 1 & Salimity & 0.0034 & -0.0035 \\ Cxygen & 0.0018 & -0.0051 \\ Temperature & -0.0006 & -0.0056 \\ Season & 0.0705 & 0.1298 \\ Elevation & -0.0185 & -0.1719 \\ DistChen & -0.0011 & 0.0002 \\ SA \# 2 & Salimity & -0.0011 & 0.0090 \\ Cxygen & -0.0024 & -0.0065 \\ Temperature & -0.0059 & 0.0045 \\ Season & 0.0497 & 0.3175 \\ Elevation & -0.0177 & -0.0046 \\ DistChen & -0.0007 & 0.00008 \\ SA \# 3 & Salimity & 0.0091 & 0.0511 \\ Oxygen & -0.0291 & 0.2020 \\ Temperature & -0.0054 & 0.0251 \\ Elevation & -0.0219 & 0.0316 \\ DistChen & -0.0004 & -0.0003 \\ \hline \end{array} $	s A #1	Solinity	0.0054	0.0055
Functional dissimilarity -0.005 -0.0011 SA#2 Salinity -0.0011 0.0002 Salinity -0.0011 0.0002 Sasis Salinity -0.0011 0.0002 Sasis Sasis -0.0044 -0.0065 Temperature -0.0059 0.0045 -0.0047 Sasis Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 -0.0291 Temperature -0.0054 0.0255 -0.0003 Functional dissimilarity Salinity -0.0047 -0.01042078 Season 0.0134 0.0696 -0.3371 DistChen -0.0047 -0.0137 0.0158 Temperature 0.0024 -0.0619 -0.0002 SA#2 Salinity </td <td>34#1</td> <td>Ovugen</td> <td>0.0018</td> <td>-0.0033</td>	34#1	Ovugen	0.0018	-0.0033
Season 0.0705 0.1298 Elevation -0.0185 -0.1719 DistChen -0.0004 0.0002 SA#2 Salinity -0.0011 0.0090 Oxygen -0.0024 -0.0065 Temperature -0.0059 0.0045 Season 0.0497 0.3175 Elevation -0.0077 -0.0046 DistChen -0.00007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0221 0.0220 - Temperature -0.0054 0.0251 Elevation Oxygen -0.00046 -0.0003 - Functional dissimilarity Salinity -0.0054 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.014 -0.0619 Oxygen -0.0137 0.0158<		Temperature	-0.0006	-0.0011
SA#2 Salinity -0.0185 -0.1719 JistChen -0.00004 0.0002 SA#2 Salinity -0.0011 0.0090 Oxygen -0.0024 -0.0065 Temperature -0.00497 0.3175 Elevation -0.0177 -0.0046 DistChen -0.0091 0.0511 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0054 0.0220 Temperature -0.0054 0.0251 Elevation -0.0219 0.0316 DistChen -0.00004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature SA#1 Salinity -0.0047 -0.01042078 Season 0.0134 0.6696 1291 DistChen 0.0001 0.00002 -0.1371 SA#2 Salinity -0.0137 0.0158 Temperature -0.0276 0.0606 28230		Season	0.0705	0 1298
DistChen -0.0004 0.002 SA#2 Salinity -0.0011 0.0090 Oxygen -0.0024 -0.0065 Temperature -0.0059 0.0045 Season 0.0497 0.3175 Elevation -0.0177 -0.0046 DistChen -0.0007 0.0008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0054 0.0251 DistChen -0.0004 -0.00003 Functional dissimilarity Salinity -0.0219 0.0316 DistChen -0.0004 -0.00003 -0.0003 Functional dissimilarity Salinity -0.0059 -0.0307 SA#1 Salinity -0.0142 -0.01042078 Season 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0137 0.0158 Temperature 0.0001 0.00002 SA#2 Salinity		Flevation	-0.0185	_0.1250
SA#2 Salinity -0.0011 0.0090 Oxygen -0.0024 -0.0065 Temperature -0.0059 0.0045 Season 0.0497 0.3175 Elevation -0.0007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0054 0.0251 DistChen -0.0004 -0.0003 Temperature -0.0219 0.0316 DistChen -0.0004 -0.0003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0317 0.0142078 Season 0.0134 0.0696 Elevation -0.010422 -0.1371 DistChen 0.0024 -0.0619 Oxygen -0.0276 0.0608 Season -0.0137 <		DistChen	-0.00004	0.0002
Shift 2 Sammy -0.0014 -0.0055 Oxygen -0.0059 0.0045 Season 0.0497 0.3175 Elevation -0.0017 -0.0046 DistChen -0.0007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0054 0.0251 Elevation -0.0219 0.0316 DistChen -0.00004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 SA#1 Salinity -0.0004 -0.00003 Functional dissimilarity Season 0.0134 0.0696 Elevation -0.0134 0.0696 Elevation Elevation -0.00482 -0.1371 0.0142078 Season 0.0134 0.0696 Elevation -0.0024 -0.0619 SA#2 Salinity -0.0024 -0.01371 0.0158 Temperature -0.0276 0.0608 Season	SA#2	Salinity	_0.0011	0.0090
Functional dissimilarity Salinity -0.00059 -0.0045 Functional dissimilarity Salinity 0.0091 0.0008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0054 0.0220 Temperature -0.00007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0004 0.0251 Elevation -0.0219 0.0316 DistChen -0.0004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Salinity Oxygen 0.0184 0.0696 Season Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0276 0.0608 Season -0.0137 0.0158 Temperature -0.0024 -0.1709 Oxygen -0.0024 -0.1709	3A# 2	Ovugen	0.0024	0.0090
Season 0.0007 0.3175 Elevation -0.0177 -0.0046 DistChen -0.0007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0004 0.0251 Elevation -0.0219 0.0316 DistChen -0.0004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen -0.0024 -0.0619 SA#2 Salinity -0.0276 0.0608 Season -0.0137 0.0158 158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.0024 -0.1709 SA#3 Sal		Temperature	-0.0024	0.0045
Elevation -0.0177 -0.0046 DistChen -0.00007 0.00008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0241 0.2020 Temperature -0.0054 0.0251 Elevation -0.0219 0.0316 DistChen -0.0004 -0.0003 Functional dissimilarity Salinity -0.0047 -0.0307 SA#1 Salinity -0.0047 -0.0142078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0616 -0.0806 Ele		Season	0.0497	0.3175
DistChen -0.00007 0.0008 SA#3 Salinity 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0291 0.2020 Temperature -0.0219 0.0316 DistChen -0.0219 0.0316 DistChen -0.0004 -0.0003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.0002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature Temperature -0.0276 0.0608 Season Salinity 0.0019 0.1038 0.055 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 0.1005 SA#3 S		Elevation	-0.0177	-0.0046
SA#3 Salinity Oxygen 0.0091 0.0511 Oxygen -0.0291 0.2020 Temperature -0.0054 0.0251 Elevation -0.0219 0.0316 DistChen -0.00004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature Functional dissimilarity -0.0024 -0.1709 0.0158 Balinity -0.0024 -0.0191 0.0055 SA#3 Salinity 0.0019 0.1038 SA#3 Salinity 0.0019 0.1038 Salinity 0.0019 0.1038 0.0251 SA#3 Salinity 0.0019 <td< td=""><td></td><td>DistChen</td><td>-0.00007</td><td>0.00008</td></td<>		DistChen	-0.00007	0.00008
Shing 5.0071 0.0011 Oxygen -0.0291 0.2020 Temperature -0.0054 0.0251 Elevation -0.0219 0.0316 DistChen -0.0004 -0.0003 Functional dissimilarity Salinity -0.0059 -0.0307 SA#1 Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature Temperature -0.0276 0.0608 Season Salinity 0.0019 0.1038 0.005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 1.1243 Temperature -0.0449 -0.0708 Elevation	SA#3	Salinity	0.0091	0.0511
Functional dissimilarity Salinity -0.0054 0.0251 Functional dissimilarity DistChen -0.00004 -0.00003 Functional dissimilarity Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.001 0.0005 SA#3 Salinity -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0276 0.0823 DistChen -0.0001 0.0005	511// 5	Oxygen	-0.0291	0.2020
Elevation -0.001 0.0316 DistChen -0.00004 -0.00003 Functional dissimilarity SA#1 Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 0.0255 0.0047 -0.01042078 Season 0.0134 0.0696 0.0002 -0.1371 0.00002 SA#2 Salinity -0.0024 -0.0619 0.00002 SA#2 Salinity -0.0024 -0.0619 0.0002 SA#2 Salinity -0.0276 0.0608 0.0608 Season -0.0137 0.0158 -0.0806 0.0005 SA#3 Salinity -0.001 0.0005 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 -0.0708 Elevation -0.0227 0.0823 1038 Oxygen -0.0227 0.0823 1038		Temperature	-0.0054	0.0251
DistChen -0.00004 -0.00003 Functional dissimilarity -0.00004 -0.00003 SA#1 Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.001 0.0005 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 1243 Temperature -0.0449 -0.0708 1243 Elevation -0.0227 0.0823 0.0233 DistChen -0.0000		Flevation	-0.0219	0.0201
Functional dissimilarity -0.0059 -0.0307 SA#1 Salinity -0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0024 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0276 0.0688 Season -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0619 0.0005 SA#3 Salinity 0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0277 0.0823 DistChen -0.0227 0.0823		DistChen	-0.00004	-0.00003
Functional dissimilarity Salinity -0.0059 -0.0307 SA#1 Salinity 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity -0.0276 0.0608 Season -0.0616 -0.0806 -0.1709 DistChen -0.0001 0.0005 -0.0037 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 -0.1708 Elevation -0.0227 0.0823 -0.0708 Elevation -0.0227 0.0823 -0.00005				
Functional dissimilarity SA#1 Salinity -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 Oxygen -0.0616 -0.0806 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0842 0.1243 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005				
SA#1 Salinity Oxygen -0.0059 -0.0307 Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen 0.001 0.0005 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0842 0.1243 Temperature -0.0227 0.0823 DistChen -0.0227 0.0823	Functional dissimilarity			
Oxygen 0.0188 0.0255 Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.0002 SA#2 Salinity -0.037 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 Oxygen -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 Season -0.0616 -0.1037 Substitution -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005	SA#1	Salinity	-0.0059	-0.0307
Temperature 0.0047 -0.01042078 Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.0024 -0.1709 SA#3 Salinity 0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Oxygen	0.0188	0.0255
Season 0.0134 0.0696 Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0806 Elevation -0.0024 -0.1709 DistChen -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 1243 Temperature -0.0449 -0.0708 Elevation DistChen -0.0227 0.0823 0.0005		Temperature	0.0047	-0.01042078
Elevation -0.0482 -0.1371 DistChen 0.0001 0.00002 SA#2 Salinity -0.024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0209 0.00005		Season	0.0134	0.0696
DistChen 0.0001 0.0002 SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0021 -0.1709 DistChen 0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0209 0.00005		Elevation	-0.0482	-0.1371
SA#2 Salinity -0.0024 -0.0619 Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		DistChen	0.0001	0.00002
Oxygen -0.0137 0.0158 Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005	SA#2	Salinity	-0.0024	-0.0619
Temperature -0.0276 0.0608 Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.001 0.0005 Salinity 0.0019 0.1038 Oxygen -0.0449 -0.1708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Oxygen	-0.0137	0.0158
Season -0.0616 -0.0806 Elevation -0.0024 -0.1709 DistChen -0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Temperature	-0.0276	0.0608
Elevation -0.0024 -0.1709 DistChen -0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0449 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Season	-0.0616	-0.0806
DistChen -0.0001 0.0005 SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Elevation	-0.0024	-0.1709
SA#3 Salinity 0.0019 0.1038 Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		DistChen	-0.0001	0.0005
Oxygen -0.0842 0.1243 Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005	SA#3	Salinity	0.0019	0.1038
Temperature -0.0449 -0.0708 Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Oxygen	-0.0842	0.1243
Elevation -0.0227 0.0823 DistChen -0.0009 0.00005		Temperature	-0.0449	-0.0708
DistChen –0.00009 0.00005		Elevation	-0.0227	0.0823
		DistChen	-0.00009	0.00005

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Appendix E

Table E.1

Summary of general linear model outputs for the ecological guilds.

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Diadromous	Habitat	2	2.3602	87	8.6283	0.3072	
	Sampling area	2	1.7442	85	6.8841	0.4181	
	Season	1	1.4773	84	5.4067	0.2242	
	Habitat:Sampling area	4	0.0000	80	5.4067	1.0000	
Estuarine	Habitat	2	20.4896	87	33.503	3.554e-05	***
	Sampling area	2	0.2320	85	33.271	0.8905	
	Season	1	0.7117	84	32.559	0.3989	
	Habitat:Sampling area	4	0.0000	80	32.559	1.0000	
Marine juvenile	Habitat	2	17.9926	87	74.784	0.0001239	***
0	Sampling area	2	0.0634	85	74.721	0.9688037	
	Season	1	1.5564	84	73.164	0.2121929	
	Habitat:Sampling area	4	2.9062	80	70.258	0.5736479	
Freshwater	Habitat	2	86.973	87	37.393	<2.2e-16	***
	Sampling area	2	1.385	85	36.008	0.5003089	
	Season	1	13.168	84	22.840	0.0002848	***
	Habitat:Sampling area	4	0.000	80	22.840	1.0000000	
Marine	Habitat	2	4.7720	87	14.410	0.0920	
	Sampling area	2	3.5964	85	10.813	0.1656	
	Season	1	0.0000	84	10.813	1.0000	
	Habitat:Sampling area	4	0.0000	80	10.813	1.0000	

Table E.2

Summary of general linear model outputs for the trophic guilds.

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Benthic invertivorous	Habitat	2	4.7720	87	14.4098	0.09200	
	Sampling area	2	1.4975	85	12.9124	0.47297	
	Season	1	3.0070	84	9.9054	0.08291	
	Habitat:Sampling area	4	0.0000	80	9.9054	1.00000	
Suprabenthic invertivorous	Habitat	2	5.2625	87	27.465	0.07199	
	Sampling area	2	4.7076	85	22.758	0.09501	
	Season	1	6.1415	84	16.616	0.01320	*
	Habitat:Sampling area	4	0.2575	80	16.359	0.99239	
Planctivorous	Habitat	2	17.4801	87	104.427	0.00016	***
	Sampling area	2	0.4969	85	103.930	0.78002	
	Season	1	1.3615	84	102.568	0.24327	
	Habitat:Sampling area	4	8.9991	80	93.569	0.06112	
Piscivorous	Habitat	2	7.8508	87	24.877	0.01973	*
	Sampling area	2	2.5168	85	22.360	0.28410	
	Season	1	3.6410	84	18.719	0.05637	
	Habitat:Sampling area	4	0.0000	80	18.719	1.00000	
Omnivorous	Habitat	2	38.206	87	82.079	5.055e-09	***
	Sampling area	2	3.647	85	78.431	0.161423	
	Season	1	0.003	84	78.428	0.955393	
	Habitat:Sampling area	4	17.139	80	61.289	0.001816	**
Herbivorous	Habitat	2	63.519	87	59.061	1.611e-14	***
	Sampling area	2	3.404	85	55.657	0.18230	
	Season	1	0.001	84	55.656	0.97513	
	Habitat:Sampling area	4	10.732	80	44.924	0.02974	*

Table E.3

Summary of general linear model outputs for the position guilds.

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Benthic	Habitat	2	4.7720	87	14.410	0.092	
	Sampling area	2	1.4975	85	12.912	0.473	
	Habitat:Sampling area	4	0.0000	81	12.912	1.000	
Demersal	Habitat	2	7.2381	87	19.068	0.02681	*
	Sampling area	2	2.2262	85	16.842	0.32854	

Table E.3 (continued)

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
	Habitat:Sampling area	4	0.0000	81	16.842	1.00000	
Pelagic	Habitat	2	2.4065	87	68.275	0.300223	
	Sampling area	2	3.1473	85	65.128	0.207284	
	Habitat:Sampling area	4	18.0874	81	47.040	0.001186	**

Table E.4

Occurences per habitat of identified species. The functional guild are shown for ecological (ER: Estuarine, MA: Marine, MJ: Marine juvenile, DIA: Diadromous, FW: Freshwater), position (B: Benthic, D: Demersal, P: Pelagic) and trophic guild (SI: Suprabenthic invertivorous, BI: Benthic invertivorous, PL: Planktivorous, O: Omnivorous, H: Herbivorous, P: Piscivorous).

Species	Functional guild			Habitat			Habitat distribution	
	Ecological	Position	Trophic	Main channel	Tidal marsh	Diked marsh		
Agonus cataphractus	ER	В	BI	1	0	0	Main channel only	
Buglossidium luteum	MA	В	BI	1	0	0		
Chelidonichthys lucernus	MJ	В	SI	1	0	0		
Ciliata mustela	ER	В	0	1	0	0		
Echiichthys vipera	MA	В	SI	1	0	0		
Limanda limanda	MJ	В	BI	1	0	0		
Liparis liparis	ER	В	BI	1	0	0		
Pleuronectes platessa	MJ	В	BI	1	0	0		
Scophthalmus rhombus	MJ	В	BI	1	0	0		
Syngnathus sp	ER	D	PL	1	0	0		
Trisopterus luscus	MJ	D	SI	1	0	0		
Aphia minuta	ER	Р	PL	1	1	0	Main channel and tidal marsh	
Merlangius merlangus	MJ	D	SI	1	1	0		
Anguilla anguilla	DIA	D	0	1	1	1	Common on the three habitats	
Clupea harengus	MJ	Р	PL	1	1	1		
Dicentrarchus labrax	MJ	D	SI	1	1	1		
Gasterosteus aculeatus	ER	D	BI	1	1	1		
Liza ramada	DIA	D	н	1	1	1		
Osmerus eperlanus	DIA	Р	SI	1	1	1		
Platichthys flesus	DIA	В	BI	1	1	1		
Pomatoschistus microps	ER	В	BI	1	1	1		
Pomatoschistus minutus	ER	В	BI	1	1	1		
Solea solea	MJ	В	BI	1	1	1		
Sprattus sprattus	MJ	Р	PL	1	1	1		
Ammodytes tobianus	ER	В	PL	0	1	0	Tidal marsh only	
Abramis brama	FW	D	BI	0	1	1	Tidal marsh and diked marsh	
Atherina boyeri	ER	Р	PL	0	1	1		
Blicca bjoerkna	FW	D	BI	0	1	1		
Carassius gibelio	FW	D	0	0	1	1		
Cyprinus carpio	FW	D	0	0	1	1		
Pseudorasbora parva	FW	Р	0	0	1	1		
Pungitius pungitius	FW	D	SI	0	1	1		
Rhodeus amarus	FW	D	0	0	1	1		
Rutilus rutilus	FW	Р	0	0	1	1		
Scardinius erythrophthalmus	FW	Р	0	0	1	1		
Alburnus alburnus	FW	Р	PL	0	0	1	Diked marsh only	
Carassius carassius	FW	D	0	0	0	1		
Esox lucius	FW	В	F	0	0	1		
Perca fluviatilis	FW	Р	SI	0	0	1		
Sander lucioperca	FW	D	F	0	0	1		
Tinca tinca	FW	D	BI	0	0	1		

Data availability

Data will be made available on request.

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