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Using simulated environmental variables to assess the seasonal estuarine habitat selection of a critically endangered anadromous species (*Acipenser sturio*)

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Abstract :

The European sturgeon (Acipenser sturio) is a critically endangered anadromous fish species with the last remaining population living in the Gironde estuary, thanks to restocking programs. Between 2010 and 2018, trawling surveys (1022 trawl tows) in the estuary caught 452 sturgeons (fork length (FL) from 25.5 cm to 154 cm). Based on previous knowledge about the species ecology, individuals have been categorized into two groups, Estuarine Dwellers (ED; FL below 68 cm) that are using mainly the estuary, and Sea Explorers (SE; FL equal or above 68 cm) that could accomplish migration at sea. ED and SE were found in the estuary at all seasons with densities being the highest in autumn for SE and in all season except spring for ED. Hotspot analyses were made at the seasonal scale to localise ED and SE concentrations. Differences were analysed according to environmental variables (temperature, water column height, salinity and concentration in suspended matters) extracted from a hydrodynamic model (MARS3D), which all contribute to fish localisation at all seasons. In all seasons, both groups were using common areas located downstream (overlap from 26 to 33%) except in autumn, when different areas were used (12% overlap). SE were encountered downstream in deeper areas with higher salinity and lower temperature (except in winter). For this group, temperature seems to be a limiting factor. ED occupied downstream as well as upstream areas with lower salinity and higher temperature in summer, but there was no habitat selection linked to simulated environmental variables in spring and autumn. Since ED are mainly using the estuary they are probably accustomed to the range of values of the abiotic variables characterising the estuary and other factors are probably at play in spring and autumn, such as prey distribution. Comparison with the location of ancient wild cohorts highlights common hotspot areas downstream with our stocked population but the disappearance of a former upstream hotspot. We explained this difference by the environmental changes witnessed by the estuarine environment in the last decades. Our results highlights important areas for both groups that could help the design of conservation measures.

Highlights

► Densities varied seasonally according to size group. ► All environmental variables tested contributed to Sea Explorers location at all seasons. ► In summer, temperature seem to be restrictive for Sea Explorers. ► No influence of environmental variables for Estuarine Dwellers in spring and autumn. ► Comparison with wild cohorts showed common hotspots downstream.

Keywords : Acipenser sturio, Estuary, Habitat, Stocking, Spatial analysis

1. **Introduction**

Habitat, for a species, can be described as a multidimensional space where suitable environmental variables are spatially and temporally dynamic according to ontogeny, seasonality or diel changes (Beck *et al.*, 2001; Leveque, 1995;

Southwood, 1977). For diadromous species, distinct habitats are needed in marine and freshwater environments for growth and reproduction and, according to the species, it can necessitate long-distance movements (McDowall, 1988). For those fish, migration and habitat selection depends on their ability to adapt to different environmental conditions. Depending on their ontogenic stage, fish can adapt through physiological mechanism such as osmoregulation or thermoregulation (Binder *et al.*, 2011).

In dynamic ecosystems, such as macrotidal estuaries, the distribution of habitat patches changes spatially over time. This environment could be described as a “shifting habitat mosaic” (Stanford *et al.*, 2005; Wimberly, 2006). These ecosystems have particularly complex habitat dynamics involving several temporal scales. Daily tidal dynamics interact with seasonal patterns of freshwater discharge, driving environmental variability (in salinity, water level, current velocity and direction) and creating high spatio-temporal habitat heterogeneity. All species living in estuaries need to develop behavioural strategies adapted to these highly fluctuating environments (Kinne, 1966). Being at the interface between salt water and fresh water, estuaries offer suitable conditions for marine, migratory and estuarine species (Elie *et al.*, 1990; Potter *et al.*, 1986). Salinity tolerance in this kind of environment is crucial. This faculty is reached through early development, gradual acclimation or can be environmentally or developmentally cued depending on the species (Zydlewski and Wilkie, 2012).

Empirical studies of habitat availability and use by species are challenging in such large dynamic ecosystems, as they require spatio-temporally explicit data acquired at appropriate scales with a sufficiently fine resolution. It became particularly promising in the view of technological developments in remote-sensing and environmental modelling because they give access to continuous environmental data with high resolution in space and time (Carbonneau and Piégay, 2012; Neumann *et al.*, 2015). Using 3D hydrodynamic estuarine or fluvial models can capture the whole range of spatio-temporal changes in fish habitat availability (Alp and Pichon, 2021; Foubert *et al.*, 2019).

The Gironde estuary, the largest estuary in Western Europe has a large fish assemblage (Lobry, 2003). Several studies were carried out to have a better understanding of the changes in the morphology (Sottolichio *et al.*, 2013) and the hydrodynamics (Diaz *et al.*, 2020) of the estuary. Other studies looked into the dynamics of highly turbid waters (Sottolichio and Castaing, 1999). This estuary also hosts the last population of European sturgeons (*Acipenser sturio*), providing them with suitable habitats for growth and a migratory corridor (Acolas *et al.*, 2017, 2012; Rochard *et al.*, 2001). *A. sturio* is an anadromous species, meaning that reproduction occurs in freshwater and juveniles migrate toward the estuary during their first year of life to grow for a few years (Acolas *et al.*, 2012; Rochard *et al.*, 2001). Individuals can leave the estuary at about 3 years old and carry out back and forth movement between the estuary and the sea. Those movements can last for several years or individuals can migrate far at sea. The adults come back to reproduce in freshwater from around 12 years old for male and 15 years old for females (Castelnaud et al., 1991; Rochard et al., 1997). It is a long-lived species, highly protected, and classified as critically endangered by the International Union for Conservation of Nature (IUCN) (Gessner *et al.*, 2022). National action plans were implemented in France and Germany (Gessner *et al.*, 2010; Ministère de l'écologie du développement durable des transports et du logement, 2011). Between 2007 and 2015, 1.7 million individuals, were born in captivity (Williot and Chèvre, 2011), and they were released in the Garonne and Dordogne rivers at different stages (larvae, 3 months old, 1 year old and more) (Roques *et al.*, 2018). We assume that all *A. sturio* present nowadays in the Gironde estuary result from stocking. For such an assisted population, a clear understanding of habitat use and of the environmental variables influencing its fitness are key components for conservation purposes (Jetz *et al.*, 2019).

However, because rare species are usually found in low densities, detection of relationships between presence or densities and environmental variables is challenging (Bowser *et al.*, 2023). Multiples methods were adapted to the evaluation of habitat use by rare species, based on different types of models (Gogol-Prokurat, 2011; McKenna Jr *et al.*, 2013). Geospatial techniques such as hotspot analysis (Getis and Ord, 1992; Ord and Getis, 1995a) can also be used to identify spatial clusters, where great concentrations of one or more species can be delimited (Nelson and Boots, 2008). In freshwater, it has been done for a sturgeon species, the lake sturgeon (*A. fulvescens*) to characterize juveniles habitats (Mettler *et al.*, 2022). Determining hotspots for estuarine fish can be difficult due to their highly variable habitat use, both spatially and temporally, and across life stages (Hanke *et al.*, 2013). Still, successful applications already exist (Bowser *et al.*, 2023; Stevens *et al.*, 2022).

This work aims at identifying and characterizing the habitat use of stocked *A. sturio* in the Gironde saline estuary, with a focus on the environmental variables at play thanks to sampling by trawling, simulated environmental variables and geospatial tools.

2. Material and methods

2.1. Study site

This study takes place in the Gironde estuary, in the South West of France (Fig. 1). It is formed by the Garonne and the Dordogne rivers and its surface of 635

km^2 makes it the biggest estuary in western Europe. (Allen *et al.*, 1977). Its depth varies between 3 and 30m in the subtidal area, where deeper areas are located at the mouth. The Gironde estuary has a macrotidal regime with a tidal amplitude ranging from 2.5 to 5.5m. Such variations in the tidal amplitude affect mixing in the estuary. Average river discharge was estimated at 803 ± $685m^3.s^{-1}$ between 2010 and 2018 (data from the calibration of the MARS3D model (Diaz *et al.*, 2020)). Silt (Ø <0.08mm) is the predominant sediment followed by sand (0.075 < Ø < 2.0) (Brosse, 2003; Sauriau and Blanchet, 2018). The limits of the sampling area of our study is shown in Figure 1, the saline estuary is considered between the confluence of the Dordogne-Garonne rivers upstream and the line between Le Verdon and Suzac Point downstream. Our sampling is located in the subtidal estuary, mainly in mesohaline sectors and it covers about 146 km^2, which represent about 32% of the saline estuary. To measure spatial location, we used Kilometric Points (KP); they are materialized as a point every one kilometre starting in Bordeaux as KP 1 and ending at the mouth of the estuary as KP 100. Our sampling area is located longitudinally between KP 45 and KP 90 (Fig. 1). According to the MARS3D model (Diaz *et al.*, 2020), between 2010 and 2018, the average salinity gradient within our sampling area ranged from 1.5 upstream to 31.5 downstream with a mean of 17.7 ± SD 9.1; temperature ranged from 4.5°C to 24.1°C with a mean of 14.6 ± SD 5.2°C and water column height ranged from 4.8m to 17.9m with a mean of 8.3m ± SD 2.1m.

2.2. Biological data

Sampling of the estuarine ichtyofauna has been carried out with a bottom otter trawl since 2009 (21m long with a decreasing mesh size from 60 to 20mm, and a maximum underwater opening of 12m of width and 4m of height), during the

STURAT field campaigns (Acolas et al., 2011). Every two months, about 20 trawl tows were conducted within this sampling area; they were distributed over 20 sampling rectangles to allow for a homogeneous coverage of the area (Fig. 2). Sampling cannot be carried over the entire estuary because of the navigation channel and the presence of wrecks and shallows. Between 2010 and 2018, 1022 trawl tows were realized, their average duration was 30 ± SD 8 min and their average length was 3.9 ± SD 0.7 km for about 12m in width. All captured fishes were identified and counted but in this work, we focus on *A. sturio* catches. Sturgeons were counted, weighed and measured. Fin samples were collected for age determination (Rochard and Jatteau, 1991) and genetic monitoring (Roques *et al.*, 2018), as well as stomach contents for diet analysis (Brosse *et al.*, 2000). Over the studied period, 450 *A. sturio* were captured with a fork length (FL) varying from 25.5cm to 154cm with an average of 67.7cm ± SD 21.1cm. The weight varied from 0.08 kg to 33.5kg with an average of 2.7 kg ± SD 3.6 kg. 163 trawl tows contained at least one *A. sturio* (*i.e.* 16% of the trawl tows). Among these trawl tows, 56% contained only one sturgeon and 34% contained between 2 and 5 sturgeons. The remaining 10 % contains 6 or more sturgeons with some exceptional events with a maximum of 36 sturgeons in a single trawl tow.

In the Gironde estuary, juveniles of *A. sturio* spend some time in the estuary before starting back and forth movement between the estuary and the sea to fulfil their growth and maturation needs (Acolas *et al.*, 2011a; Castelnaud *et al.*, 1991; Rochard *et al.*, 1990). Considering our current knowledge (Castelnaud and Trouvery, 1984; Rochard et al., 2001, Rochard et al., 1997) we assumed that 3-years old would be the age at which most individuals can begin to move periodically to and from the ocean. We also hypothesise that change in habitat selection occurs at that age and we consider two groups, below and above 3-years old. Since age reading was not available for all individuals, we used the corresponding average length of 3-year old fish (*i.e.* 68cm FL) as a threshold to separate the two groups: one with individuals below 68 cm FL (N = 251, mean FL = 53.9 ± SD 9.1cm), mostly composed of fish resident in the estuary, called in this work estuarine dwellers (ED), and one with individuals with a FL equal or above 68cm (N = 199, mean FL = 85.4 ± SD 18.5cm), composed of fish that can regularly migrate between the estuary and the sea (referred to as SE, sea explorer in this work).

2.3. Environmental data

2.3.1. Environmental variables sampled at the trawl tow scale

At the beginning of each trawl tow, environmental variables were recorded about 1.5m above the bottom with a probe (YSI 6600 V2 before 2013; Hydrolab miniprobe 5 since April 2013). The average values of the variables within the studied period were: temperature (15.83 ± SD 5.60 °C), salinity (14.44 ± SD 6.86) and dissolved oxygen (8.73 ± SD 1.60 mg/L). The average depth at the beginning of the trawls was (7.40 ± SD 2.03 m).

2.3.2. Hydrodynamic simulated variables at the Gironde estuary scale

To characterise the spatiotemporal environmental context of the trawl tows, a process-based hydro-sedimentary model of the Gironde called MARS3D was used (Diaz *et al.*, 2020; Lamarque *et al.*, 2022, 2021). This model enables a spatiotemporal continuous environmental characterisation of the estuary between 2010 and 2018 at a 1h temporal resolution (30min for temperature) with cell size ranging from 145m x 500m at the confluence of the Dordogne and Garonne rivers to 400m x 600m at the mouth of the estuary; the cell size within our sampling area ranges between 320 x 530m and 140 x 470m (Fig 2). The model provides a vertical spacing discretized into 10 equidistant sigma layers for the water column and 6 layers in the sediment column.

Temperature (°C), salinity, bottom current velocity (m.s^{-1}, calculated as $\sqrt{UZ^2 + VZ^2}$) where UZ and VZ are the along and across-estuary velocity components, respectively), water column height (WCH, m) and suspended sediment quantity (in kg/m^3 - mud, very fine sand, fine sand, medium sand and gravel concentration used as a proxy for suspended matters) were extracted from the bottom layer of the water column at the time of each trawl tow. Model results in the grid that were involved in the trawl tow were averaged within a 1h period surrounding the trawl tow (Fig. 2). Bed sediments fractions (mud, very fine sand, fine sand, medium sand and gravel) were calculated for the first four layers of the sediment column (representing 11.6cm depth). Then sediment fractions were calculated for each layer by dividing the concentration of one sediment type by the sum of all sediment types. Sediments fractions for the four layers were calculated as the sum of the fraction of one sediment type multiplied by the thickness of each layer.

2.4. Data analysis

To represent the evolution of densities of the two size groups between 2010 and 2018, density was calculated for each trawl and, for each group, by dividing the number of *A. sturio* caught by the surface of the corresponding trawl tow in square kilometres (km^2) before the density of all trawl tows was averaged for each year.

To illustrate and analyse the spatial and temporal pattern in density data of *A. sturio* in the Gironde estuary, we used spatial statistics tools: the hotspot analysis (Getis and Ord, 1992; Ord and Getis, 1995a). This analysis identifies spatially distinct areas of intense biological utilisation using density data for both size group at annual and seasonal scales. The seasons were divided using the following dates: spring from 20th of March to 20th of June; summer from 21st of June to 22nd of September; autumn from 23rd of September to 21st of December: winter from 22nd of December to 19th of March.

For both size groups, hotspots of sturgeons densities were calculated using the Getis-Ord statistic (G_i) (“Getis-Ord G_i*” function in spatial analyst ArcGis, version 10.8.2). This statistics is based on the aggregation of weighted elements within a radius of distance and measure the degree of association that results from that aggregation (Getis and Ord, 1992; Ord and Getis, 1995b).

Statistically significant clustering of trawl tow densities at a given distance of 500m (adapted to MARS3D grid) were identified using p-values (<0.05) and z-scores (>0.9). Buffers of 500m were created around each trawl tow delineating hotspot areas. Then, total surface of hotspot areas for each size groups and their overlap was calculated using ArcGis. Overlaps (in %) between size groups were calculated by dividing the surface of the overlap by the overall surface of all hotspots per seasons. Occurrences of sturgeons were calculated using the number of presence divided by the total number of trawl tows for each season.

MARS3D variables from the water bottom layer (temperature, salinity, bottom current velocity, WCH, concentration in suspended matters) and in the sediment column (mud, very fine sand, fine sand, medium sand and gravel) were extracted at annual and seasonal scales for the nine-year-period studied. Then, we allocated average values of each MARS3D simulated environmental variable to four categories: the hotspots of ED, the hotspots of SE, the hotspots of SE & ED (overlapping hotspots) and the sampling area outside hotspots (named later as the recalculated sampling area (SA)) which corresponds to the intersection of each trawl tow and the MARS3D grid.

With the simulated environmental values of the bottom layer of the water column associated with each hotspot category, we performed a Principal Component Analysis (ACP; Jolliffe, 2002) using the RStudio software (version 1.4.1103) with the packages “FactoMineR” (Lê *et al.*, 2008) and “factoextra” (Kassambara and Mundt, 2020). This analysis shows the association between the environmental variables and the hotspots of sturgeons. Next, a Non Parametric Multivariate Analysis of Variance (NPMANOVA; Anderson, 2001) was carried out with a post-hoc test (pairwise Adonis) using the function “pairwise.adonis” (Martinez Arbzu, 2017). These tests show if there is any significant difference between the 4 categories, and if so, between which categories.

Kruskall-Wallis tests (Kruskal and Wallis, 1952) and Dunn tests (Dunn, 1964) were carried out to highlight the influence of each environmental variable on the different categories.

For the sediment fractions, we used a chi-squared test (Agresti, 2018; Pearson, 1900) to determine the contributions of the different fractions to habitat selection by the size groups.

Ethical statement: The care and use of animals for this experiment complied with animal welfare laws, guidelines and policy conventions of the French national committee for ethical considerations on experiments with animals (Comité National de Reflexion Ethique sur l’Expérimentation Animale) under the authority of the Ministry of Higher Education and Research. Our sampling was approved under the following number: approval APAFiS #24931-2020040117582634-v2.

3. Results

3.1. Simulated environmental data MARS3D vs local measurements during sampling

The common environmental variables between simulated environmental MARS3D and local measurement during the STURAT sampling were temperature, salinity and WCH/depth. Salinity ranged from 0.02 to 33.1 (mean 17.7 ± SD 9.1) for MARS3D and from 0.1 to 30.4 for STURAT (14.4 ± 6.8). Temperature ranged from 4.5 °C to 24.1 °C (14.6 ± 5.2°C) for MARS3D and from 5.4°C to 24.8°C (15.9 ± 5.6°C) for STURAT. WCH ranged from 4.8m to 17.9m (mean 8.4 ± SD 2m) and depth ranged from 1.9m to 16.5m (mean 7.6 ± SD 2m) (Fig. 1; supplementary material).

3.2. Composition of the estuarine fraction of the population

The average densities per year for the two size group are illustrated on Figure 3. There is an important inter-annual variability with the highest cumulated densities encountered between 2013 and 2015. Over time, the composition of the estuarine fraction of the population tends to change with a dominance of ED progressively replaced with a higher density of SE. The highest density of ED occurred in 2014 and then decreased sharply. For SE, the highest density was estimated in 2015.

3.3. Spatial representation at the annual scale

When focusing on the presence/absence information and looking across all years, there were *A. sturio* observations all over the sampling area (Fig. 4). Overall, ED were located, longitudinally all over the sampling area from KP 90 to KP 45 while SE were located more downstream, between KP 70 and 90 most of the time, with some exceptions in 2014, 2016, 2017 and 2018 where some presences were observed between KP 57 and 70. Looking at the hotspots, ED were located between

KP 57 to 90, the most upstream hotspots being observed in 2014 and 2015 when overall densities were at their highest according to Figure 3. SE hotspots were located mainly between KP 75 to 88, the most upstream being observed in 2016 (KP 58 to 63). Both groups shared hotspots between 2010 and 2015 and in 2017 mainly downstream between KP 72 to 83. Since 2016, hotspots in the sampling grid along the left bank of the estuary were observed for ED and in 2018 for the SE also.

3.4. Interannual variations of the environmental variables

Except for bottom current velocity and WCH, environmental variables varied through the years. Between 2010 and 2018, annual average temperature varied from 12.6°C to 15.5°C. 2012 and 2015 were the coldest years (12.6 ± SD 5°C and 12.7°C ± SD 5.1°C respectively) and 2016 was the warmest year (16.3 ± 5.2°C). The others years water mean temperature was around 15°C. Standard deviation was constant through the years (≈5°C).

Annual average salinity varied from 15.7 to 20.7. The lowest mean salinity was recorded in 2013 (15.7 ± SD 9.1) and the highest salinity was recorded in 2012 (20.7 ± SD 8). For the other years, salinity was around 17.5. Standard deviation was constant through the years (≈ 9) except for 2010 when it was lower (7.4) and 2015 when it was higher (10.3).

The concentration in suspended matters varied from 0.4 kg/m^3 to 0.84kg/m^3. The lowest concentrations were recorded in 2010, 2017 and 2018 (0.49 ± SD 0.4kg/m^3; 0.41 ± SD 0.4 kg/m^3 and 0.46 ± SD 0.4kg/m^3 respectively) and the highest concentrations was recorded in 2014 (0.83 ± SD 0.7kg/m^3); the higher the concentration, the larger the standard deviation. The other years, the concentration was around 0.7 kg/m^3.

3.5. Spatial analysis at the seasonal scale

When focusing on the presence/absence information, there was *A. sturio* detection all over the sampling area (Fig. 5). Sturgeon occurrences (*i.e.* number of trawl tows with presence / total number of trawl tows) varied between 13% in spring and 22% (14% and 17% during summer and autumn respectively) but the differences were not significant (Chi-squared test; p-value = 0.24). The total number of individuals caught varied between 81 in winter and 155 in autumn. Concerning sampling effort, summer tended to be oversampled (30% of the trawl tows) and winter under sampled (18% of the trawl tows) compared to spring and autumn (27% and 25% of the trawl tows respectively).

During springtime, there was an important concentration of hotspots of both size groups downstream, within the right bank of the sampling area, from KP 76 to KP 88 with a large surface overlap between groups (33%). Two hotspots of ED were observed as well, one on the left bank between KP 76 and 80, and one upstream (KP 55 to 60).

During summer, hotspots of ED were located upstream (KP 55 to 60) but also downstream (KP 77 to 83) whereas hotspots of SE were located only downstream between KP 73 and 88. The downstream hotspots of ED (KP 77 to 83) overlapped with hotspots of SE (29% of surface in common).

During autumn, the hotspots were located along an important longitudinal gradient within the right bank (KP 70 to KP 88). The SE used mainly areas from KP 77 to KP 88, while the ED were located within three hotspots: one upstream from KP 56 to KP 60, one from KP 70 to 77 and one between KP 72 and KP 80 but closer to the right bank so it did not overlap the SE hotspots. The two size groups overlap over the smallest surface observed (12%) between KP 77 and 82.

During wintertime, like in autumn, the hotspots were located along an important longitudinal gradient within the right bank (KP 71 to KP 90) with two main areas with overlapping surfaces between the two groups (26%); one upstream between KP 56 and 61 and a longer one downstream between KP 75 and 83. Hotspots of ED were scattered with two side by side hotspots between KP 72 and 75 and one hotspot far downstream between KP 83 and 87. Hotspots of SE were mainly located between KP 75 and 83 on the right bank and one hotspots were located far downstream on the left bank between KP 85 and 89.

For SE, the highest densities within the hotspots were observed in autumn and spring (average of 6.5 ind/km² and 3.6 ind/km² respectively), whereas it decreased in summer and winter (average of 3.1 ind/km² and 2.3 ind/km² respectively).

For ED, the highest densities within the hotspots were observed in winter, summer and autumn (6.3 ind/km², 6.1 ind/km² and 5.7 ind/km² respectively) and lowest average densities were observed in spring (3.1 ind/km²).

3.6. Analysis of the influence of the environmental variables

For the four seasons, the PCA showed that the tested variables contributed to the first dimension at more than 76%. All variables tested contributed similarly to the distribution of sturgeons (Fig. 6 (a), (b), (c), (d)). Temperature and salinity as well as concentration in suspended matters were highly correlated (Fig. 2; supplementary material) with an upstream-downstream gradient within the sampling area for salinity (Fig. 3; supplementary material). For temperature the gradient exists also in spring and summer with higher temperature upstream the sampling area, and it is less pronounced in autumn and winter with a higher variability in upstream (Fig. 5; supplementary material). Concentration in suspended matters vary though season with higher concentration upstream during spring (Figs. 2 & 4; supplementary material). WCH was not correlated to any other variables and did not vary through seasons within the sampling area (Figs. 2 & 6; supplementary material). The deepest areas were downstream above KP 86 and the highest bottom velocities were upstream, above KP 66 (Figs. 6 -7; supplementary material).

Within the sampling area, environmental variables differed according to seasons: average temperature was highest in summer (20.8°C) and then in spring (14.8°C); average salinity was highest in autumn (18.8) then summer (16.5) and concentration in suspended matters was highest in winter and spring (about 0.3 kg/m^3) (Fig. 7 (a), (b), (c), (d)). Average temperature dropped to 8.9°C in winter (Fig. 7 (d)) and average salinity dropped to 10.7 in spring (Fig. 7 (a)). Considering the environmental variables in the water column mentioned above, for all seasons, SE hotspots were always significantly different from the recalculated sampling area (SA) (Table 1). However, it varies accordingly to the season for ED whose hotspots were significantly different from SA in summer and winter but not in spring and autumn (Table 1). SE and ED hotspots were all significantly different whatever the season. The overlap ED & SE hotspots were significantly different from SA in all seasons except in winter, from SE in all seasons except in spring and from ED in all seasons (Table 1).

Concerning the sediment fractions, no significant difference were found between the groups in all seasons (p-value > 0.05) (Fig. 9; supplementary material). The three sand categories (very fine sand, fine sand, medium sand; Ø from 0.1mm to 0.4mm) were the main substrate available in the sampling area and used by the sturgeons. Mud (Ø<0.03mm) and gravel (Ø>3mm) were less represented in the model (Figs. 8 & 9; supplementary material).

3.6.1. Spring

During spring, ED used a wide range of environmental variables all together not significantly different from the SA. Hence, ED used areas with slightly higher temperature, concentration in suspended matter and bottom current velocity, and slightly lower WCH and lower salinity compared to SA (Fig. 8 (a), Table 1; supplementary material). SE used areas with the same range for concentration in suspended matters and bottom current velocity as SA. But salinity, and WCH were significantly higher and temperature was slightly lower than SA and ED (Figs. 7 & 8 (a), Table 1; supplementary material).

3.6.2. Summer

SE and ED used areas where environmental conditions were different from the ones in the SA. SE were located downstream in deeper areas where temperature, concentration in suspended matters and bottom current velocity was lower, and salinity was higher than SA. ED were located mostly upstream where conditions were the opposite to the ones used by SE. ED used shallow areas with high temperature, concentration in suspended matter and bottom current velocity and low salinity. (Figs. 7 & 8 (b), Table 2; supplementary material).

3.6.3. Autumn

ED used areas with the same range of salinity, WCH and concentration in suspended matters as SA but with slightly higher temperature and bottom current velocity. SE used different areas than ED, which also differed from the SA with lower temperature, concentration in suspended matters and bottom current velocity, and higher salinity and WCH (Figs. 7 & 8 (c), Table 3; supplementary material).

3.6.4. Winter

ED used areas with the same range of WCH as SA but with higher temperature and salinity and lower concentration in suspended matters and bottom current velocity. ED and SE used the same range of salinity, temperature and bottom current velocity, which are higher than SA for temperature and salinity and lower for bottom current velocity. SE used slightly deeper areas with lower concentration in suspended matters than ED (Figs.7 & 8 (d), Table 4; supplementary material).

4. Discussion

During the studied period, we observed an increase and then a decrease in the number of individuals considered as ED. This is consistent with the stocking history of young-of-the-years, which occurred only between 2007 and 2014 and then was stopped, with no sign of natural spawning (Roques *et al.*, 2018). Thus, the last cohort from 2014 cohort reached the age of 3 in 2017 (*i.e.* ED become SE). That year already showed a low density of ED (4 times less than in 2015 where cohort from 2012 to 2014 were still present). In 2018 the density decreased again (almost 10 times less than in 2017). Consequently, the number of SE increase as the fish grew and they became the main component in samples at the end of the studied period. This fact is to be considered when one looks at the annual maps but it probably does not affect the seasonal analysis.

4.1. Inter-annual variations

The analysis of hotspots at the annual scale was mainly descriptive to illustrate the inter-annual variability since the variability in the number of individuals sampled each year (from 18 to 90) prevented any statistical analysis. Generally, the area closest to the mouth of the estuary (between PK 70 and PK 90 *i.e.* 30 km and 10 km from the ocean) corresponded to the highest densities observed. Besides, the use of the most upstream areas (between PK 55 and PK 68 *i.e.* 30 and 45 km from the ocean) did not occur every year. This may be interpreted by a more consistent suitability of the lower part of the sampling area due to either environmental variables or prey location. The apparition of hotspots in the most upstream areas took place in the years 2014 and 2015, which also corresponded to the highest densities noted. It was in 2015 that an exceptional catch event happened, with 36 sturgeons caught in one trawl tow. This larger spread of ED could be explained by the need for more space as the sturgeon density increased in the estuary, inducing competition for food. During 2014, Vega (2016) highlighted a shift in the preferred prey in the stomach contents of sturgeons which was probably linked to different prey dynamics of that year; the annelids polychaete *Heteromastus filiformis* was replaced by *Boccardiella legerica*. 2016, 2017 and 2018 were also remarkable years as we observed the use of the left bank by ED and SE. 2016 was one of the warmest years, 2017 was one of the years when the freshwater front was the lowest and 2018 did not show any particularity in terms of abiotic conditions. Hence, changes in abiotic factors could influence the inter-annual distribution of the sturgeons but the observed distribution could also be linked to prey dynamics or even stochasticity.

4.2. Seasonal analysis

Using simulated environmental variables allows characterizing the estuary at a large spatial and temporal scale and contextualizing the biological data. The cell grid of MARS3D was at least ten times larger than a trawl tow, but the trawl tow intersects several cells. Comparisons of the shared environmental variables (*i.e.* salinity, temperature and water level) from our two data sources (MARS3D vs STURAT) has shown that the range of MARS3D variables was coherent with the STURAT variables ranges (Fig. 1; supplementary material). In addition to the scale differences between the two types of measurements, the difference can be partly attributed to the measurement protocol during sampling since measurements were made only at the beginning of the trawl, this one lasting 30min. Some variables can vary during this time since the tide influence is important in the estuarine environment. Hence, the simulated variables captured a broader spatial context than the trawl tow. This scale is also more consistent with the hotspot analysis. In addition, the model provides a global characterization of the studied area. The temporal scale of the model (every hour or 30min) allows characterising variables at the seasonal or annual scale and follow their variations during the study period. However, the level of confidence in the simulated variables differs. The most reliable variables are in the water column: in descending order, the hydrodynamic variables (current, water column height, tide), then the hydrological variables (salinity, temperature), then the concentration in suspended matters. The least reliable variables concern the sediment bed, because the model tends to erode the bottom too much to maintain sufficient turbidity levels, which can lead to an overestimation of the sandy bottom. Moreover, the granulometry used in MARS3D is calibrated according to the particles falling velocity, and the threshold to classify the categories of sediment can be different from the ones usually used such as the EUNIS classification (European Nature Information System) (European Environment Agency, 2004).

Our study showed that SE select their habitat within the sampling area in all seasons. This is also true for ED in summer and winter but not in spring and autumn when they did not seem to respond to any specific environmental variable within the study area. Areas of overlap between SE and ED also showed signs of selection, except in winter. However, when looking at habitat use, it is also important to keep in mind that some variables were correlated, in particular because of the upstream/downstream gradient.

In summer, SE were at their lowest densities downstream the sampling area. It suggests that most SE were at sea. ED were at their highest densities during this season with most ED located downstream sharing the same hotspots as SE; the upstream hotspot of ED gathering 4 times less individuals. Both SE and ED may avoid the highest temperature since there was a gradient of the temperature in the estuary and most individuals were located in the area with a range of temperature bewteen 17 and 20°C, avoiding the area with a range between 20 and 23°C (Fig. 5; supplementary material). Even though there is little evidence about the thermal optimum of *A. sturio*, an experiment on a small number of one-year-old juveniles (about 27cm) suggested an optimum between 12.5 and 18.5°C with a median at 16.1°C (Staaks *et al.*, 1999). At sea, a habitat study highlighted an optimum around 14-15°C and temperature around 10-11°C seems to be restrictive, but those values correspond to the interranual average of simulated variables (Charbonnel *et al.*, 2023). Ecology of the Atlantic sturgeon (*A. oxyrinchus*), a closely related sturgeon species with an optimum temperature estimated at 18°C, confirms the hypothesis that temperature is limiting (Breece *et al.*, 2018). Above 18°C, metabolic demand increases sharply in polyhaline waters (Niklitschek and Secor, 2009) and it was suggested that this response may drive the Atlantic sturgeon to seek out cooler waters during the summer months (Hightower *et al.*, 2002; Moser and Ross, 1995). Moreover, an overlap in summer habitat used by age-0 and age-2 *A. oxyrinchus* individuals had also been described in estuarine environment (Hatin *et al.*, 2007). This reinforces the idea that the summer distribution could be driven by temperature. In *A. oxyrinchus*, use of less suitable habitats in terms of temperature and salinity had been observed but only when food was available in these habitats. Otherwise, the energetic cost of tolerating those conditions would be too high (Moser and Lindley, 2007). From a conservation point of view, habitat suitability in the Gironde estuary in the summer months could be limited. Under the current regime of global warming, future summer conditions may soon be too restricting for sturgeons to keep using estuarine waters and may lead them to remain at sea to find more suitable conditions.

In autumn, ED and SE chose different areas within the estuary (lowest overlap estimated), SE were located in one large hotspot downstream and ED were split between three hotspots more upstream or closer to the right bank. SE densities were at their highest and ED densities were high too. SE favoured higher salinities and cooler temperature while ED selected lower salinity but warmer temperatures in shallower areas (Fig. 8). A telemetry study on one year-old fish showed a selection of depth within the same range as ED as well (5-8m) (Acolas *et al.*, 2017). The decrease in temperature in autumn (between 12 and 14°C all over the estuary) may have allowed more SE to use the downstream estuary. Moreover the high densities of SE may have lead the ED to spread to limit the competition; we can notice that one hotspot of ED is positioned in the continuity of the SE hotspot. When fish density is high and food density is low, agonistic behaviour and expression of dominance can be observed (Kynard and Horgan, 2002; Miheyev, 1996; Noakes and Grant, 1986). Experiments in hatchery-reared shortnose sturgeons (*A. brevirostrum*) showed a dominance of large sturgeons (average total length = 10.6cm) on small ones (average total length = 6.1cm) during competition for foraging space (Kynard and Horgan, 2002). For Atlantic sturgeons (*A. oxyrinchus*), large individuals tended to occupy more often the optimal foraging area than small individuals, even though the difference was not significant (Kynard and Horgan, 2002).

In winter, SE and ED chose quite similar areas (high overlap) but SE were at their lowest densities while ED were still at high densities. SE selected the most salty, deepest and warmest areas corresponding to the downstream area (Fig. 8). They also used the left bank which was not observed in the other seasons. Most SE may be at sea or downstream in the mouth of the estuary. In a north-eastern American estuary (Penobscot River), *A. oxyrinchus* of 120cm FL on average spend the majority of their time (67-84%) in the mesohaline part. This selection was mainly influenced by the location of the highest densities in prey (spionid polychaete worms). As for *A. sturio*, seasonal differences were also observed. *A. oxyrinchus* aggregated at the mouth of estuaries in spring and fall and used marine habitats during winter (Altenritter *et al.*, 2017; Dunton *et al.*, 2010). Moreover, during winter in Gironde, polychaete density start to naturally decrease in winter (mortality and predation following reproduction during spring and summer) (Sautour and Baron, 2020).

In spring both ED and SE were split in several hotspots with a high overlap downstream; densities of SE and ED were at the lowest. During spring, salinity is lower in the estuary, like in winter, so SE may be in downstream parts of the estuary in higher salinity environment, some deep areas are also present just downstream of the sampling area (Fig. 6; supplementary material). ED used the left bank, which was not observed in the other seasons. Their low densities suggest they may use areas outside of the sampling area.

Over all seasons, SE used downstream areas of the estuary with seasonal variations. Environmental variables in those areas are different from the ones upstream because of the natural gradient within the estuary, but those variables also vary less over the seasons in downstream areas. Hence, this may explain why they can be more suitable since the fish are coming from the ocean where conditions are more stable than in the estuary. This result is consistent with the habitat use of other sturgeon species such as *A. oxyrinchus* (Breece *et al.*, 2018) and *A. medirostris* (Moser and Lindley, 2007); big individuals (>100cm) use habitats with high salinity, at the mouth of estuaries. Furthermore, for *A. medirostris*, individuals used estuarine waters in summer and autumn but were absent in winter when temperature and salinity decreased (below 10°C and 25 PSU) (Moser and Lindley, 2007). Seasonal movements were confirmed using satellite tags on Atlantic sturgeons; during winter, sturgeons occupied deeper areas out of the Bay of Fundy and travelled back into shallower areas of the Minas Basin during spring and summer. Between November and April, mean depth occupancies ranged from 40 to 100m, which suggested migration at sea (Beardsall *et al.*, 2016; McLean *et al.*, 2014).

SE used the deepest areas of our sampling area; this may be related to their ability to migrate at sea and the associated conditions of deeper areas with higher pressure. Charbonnel et al., (2023) showed that *A. sturio* at sea find suitable depths around 30-60m. The utilisation of the same depth range was also observed in adult *A. oxyrinchus* (Altenritter *et al.*, 2017; Beardsall *et al.*, 2016; Collins and Smith, 1998; Dunton *et al.*, 2010; Stein *et al.*, 2004a, 2004b; Taylor *et al.*, 2016; Timoshkin, 1968). Since those fish can live at sea, their movements back to the estuary are induced by more favourable conditions in the estuary than at sea for some seasons (temperature or prey availability). Concerning ED, the ranges of environmental variables was wider as they used areas downstream but also upstream. The observed hotspot of ED around KP 60 in all seasons are consistent with one-year-old home range identified using telemetry in the Gironde estuary (Acolas *et al.*, 2017).

Variations in seasonal densities could also suggest that ED and SE use areas outside of the sampling area (low density in winter for SE and in spring for ED). SE could choose to stay in the ocean to limit energy costs related to osmoregulation, whereas ED, which mainly live in the estuary, are tolerant to salinity variations (Rochard *et al.*, 2001). A fraction of them (the smallest) may even prefer lower salinity, upstream, outside of the sampling area. We can assume that the estuarine environment suits ED for their growth most of the time and during the seasons where they do not select particular environmental conditions (*i.e.* spring and autumn). It is the prey location and the corresponding searching behaviour that probably drives their location. Variations in seasonal densities are also observed in the preferential preys of *A. sturio*. Diet studies showed that the preferential preys of *A. sturio* in the Gironde estuary are annelids polychaete and small crustaceans (*i.e.* isopods) to a lesser extent (Brosse *et al.*, 2000; Vega, 2016). For Acipenseridae, studies showed that their presence was related to high abundance of annelids polychaete (Acolas *et al.*, 2017; Brosse *et al.*, 2000; Hatin *et al.*, 2007; McLean *et al.*, 2013; Taverny *et al.*, 2002). During winter, a recovery phase of the polychaete community takes place, which explained the decrease in benthic species (Bachelet *et al.*, 1997; Vega, 2016) and the low number of prey consumed by sturgeons (Brosse, 2003; Vega, 2016). Then, during spring and summer, rates of recruitment of polychaetes are at their highest (Can Yılmaz *et al.*, 2009; Vega, 2016). These variations concurred with the variations in density of SE. Hence, the highest density of ED observed during winter could be more explained by environmental conditions, which are more suitable, than prey distribution.

In the Gironde estuary, polychaetes are in high abundance in subtidal areas around KP 75-85 and around KP 50-60 (Sautour and Baron, 2020) which coincide with the location of ED and SE all seasons. According to the EUNIS typology, polychaete are found in mud (A5.32) and sand (A5.22) (European Topic Centre on Biological Diversity, 2012), which are the main sediments composing the sampling area (Sauriau and Blanchet, 2018). When looking at the sediments fractions from the MARS3D model, the sampling area is mainly composed of sands, but this difference is caused by the different sediment categorisation used between EUNIS and MARS3D. However, in both cases, sediments in the sampling area were homogenous, and the absence of significant results in the sediment analysis could indicate that the sediments in the sampling area as a whole were adapted for sturgeons and their preys.

4.3. Comparison with wild population

Early works on wild *A. sturio* first described the Gironde estuary as a migration corridor (Magnin, 1982), until Rochard (2001) highlighted the use of two areas of different salinity situated around KP 55 and KP 75. Brosse (2003) also observed juveniles in high densities at three different salinity levels situated around KP78, 55 and 58. Like for the wild population, stocked individuals in our study selected the same two preferential areas highlighted by Rochard (2001). Downstream areas were used by both SE and ED and upstream areas by ED in our stocked population. However, the third area identified by Brosse (2003) located much further upstream (around KP 47) was not identified for the stocked population. Also, the stocked population used the left bank between 2016 and 2018, but also in spring and winter which had rarely been observed in the wild populations. These differences may be caused by degradations of these habitats: the wild population was studied between 1982 and 2003 and in 2010-2018 the location of the estuarine turbidity maximum had changed and was located more upstream (Sottolichio *et al.*, 2013). The Gironde estuary has also undergone two climate caused abrupt shifts in 1987 and 2001. They altered biotic and abiotic factors and caused warmer temperature, acceleration in the salinity increase, decrease in river discharge but also lower densities in some fish species. It also modified the abundance of the zooplankton, and eventually the trophic chain (Chaalali *et al.*, 2013). Between the three inter-shift periods, modification in the fish community structure, environmental drivers and fish-environment relationships have also been observed (Chevillot *et al.*, 2016). Thus, we may suggest that differences observed with wild cohorts may not be linked to the fact that fish were stocked but due to environmental changes over time within the estuary.

5. Conclusion

Our study showed influences of environmental variables on the seasonal habitat use of *A. sturio* in the Gironde estuary, which depend on the size of the sturgeons. Differences between size groups were found in all seasons. Bigger fish use stable deep downstream areas with higher salinity whereas smaller fish occupy downstream as well as upstream areas, with no particular selection in spring and autumn. The use of a hydrodynamic model is an innovative and efficient way to study the estuarine habitat use of *A. sturio*. We think the method is promising to be applied in other estuaries for rare species.

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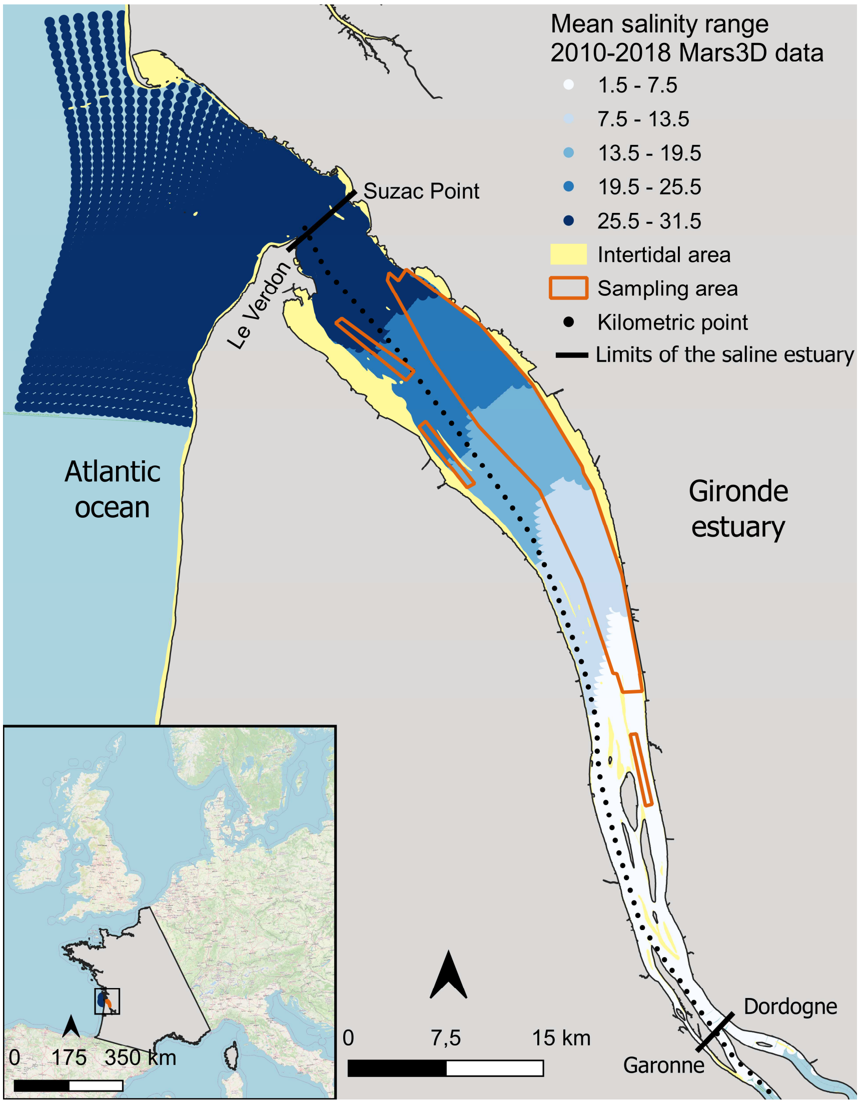


Figure with colours

Figure 1: Sampling area within the Gironde estuary with an illustration of the average salinity range.

Kilometric points are materialized as a point every kilometre starting in Bordeaux (at the Stone Bridge) as KP 1 and ending at the mouth of the estuary at KP 100.

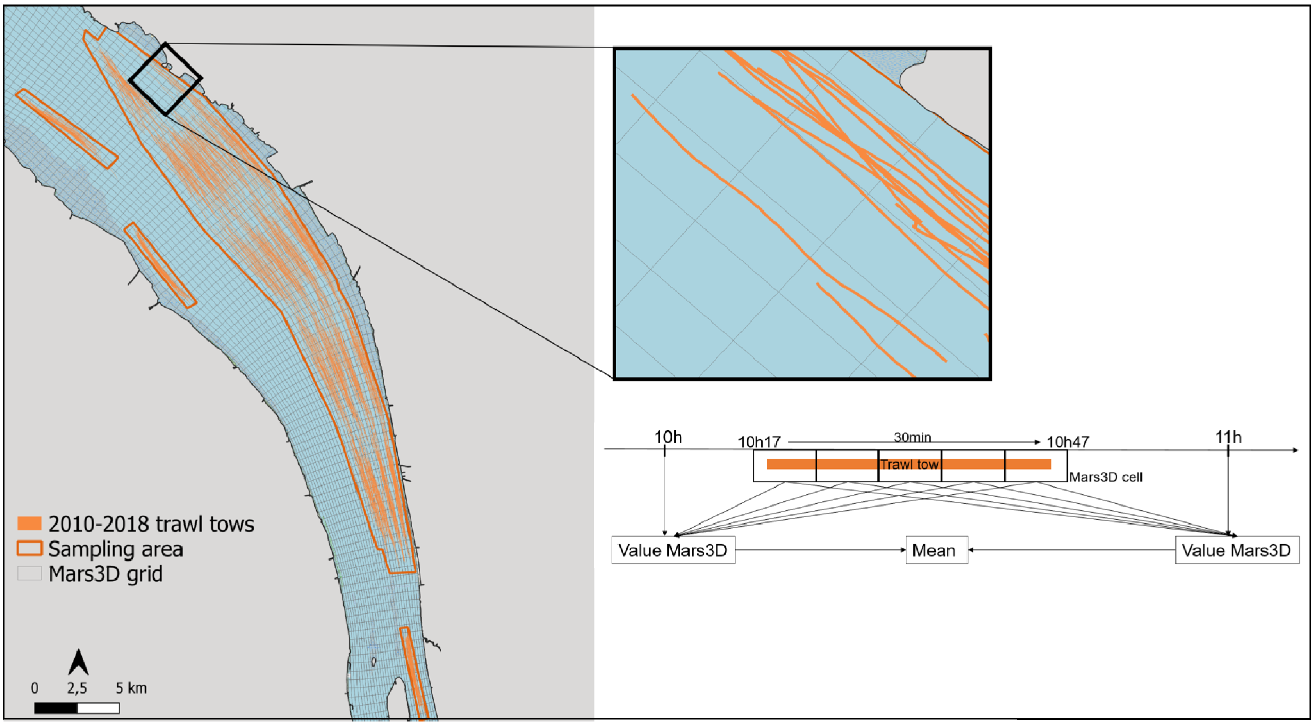


Figure with colours

Figure 2: Trawl tows within the sampling area and Mars3D cells representation for environmental variables calculation at the trawl tow scale.

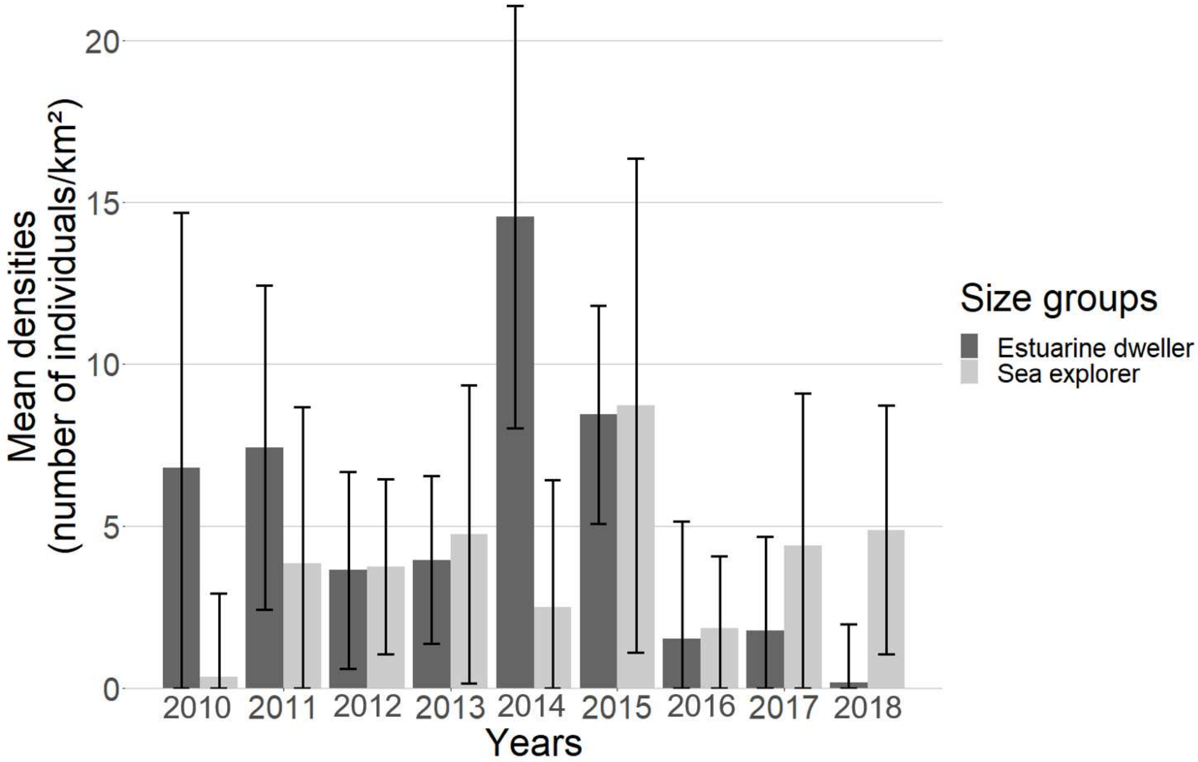


Figure 3: Evolution of *A. sturio* annual mean densities over time calculated at the level of the trawl tows for the two size groups.
The vertical bars correspond to standard error

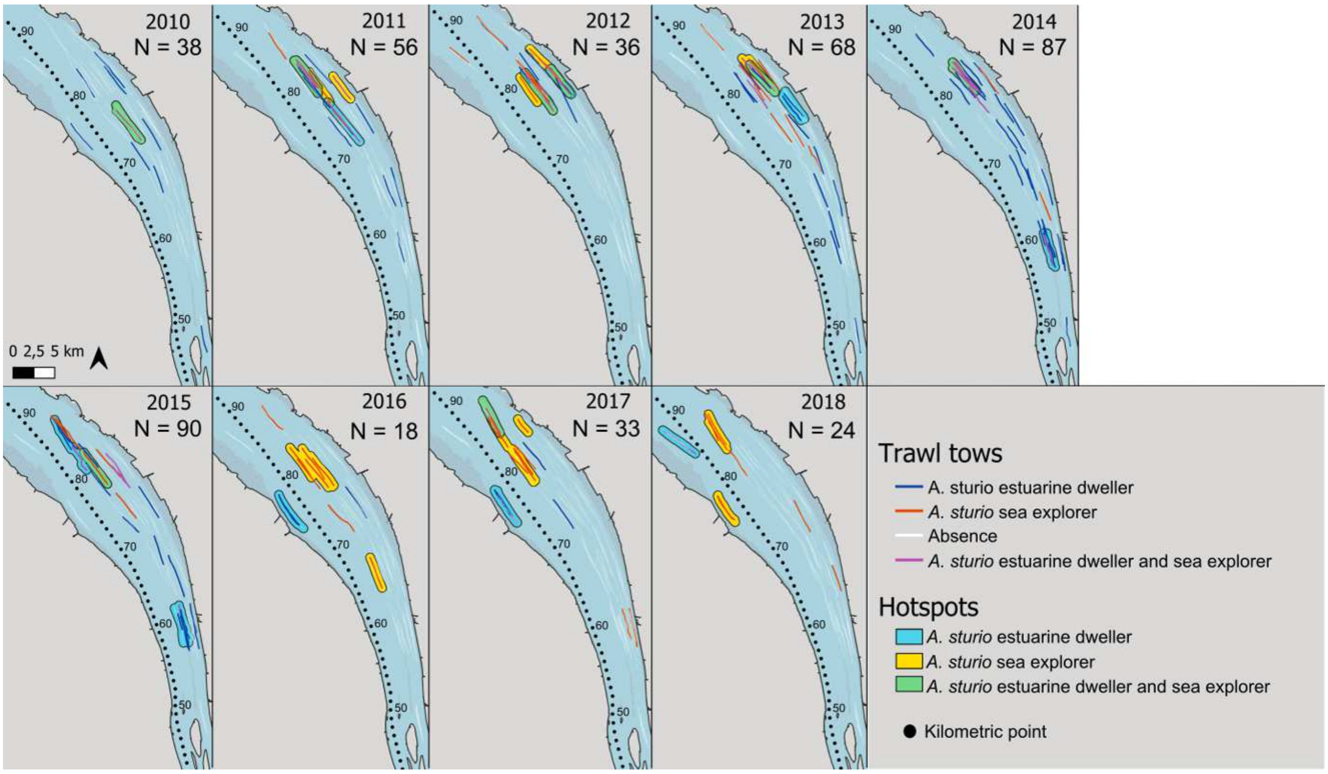


Figure with colours

Figure 4: spatial representation of the trawl tows and of the hotspots at the annual scale between 2010 and 2018.

Kilometric points are materialized as a point every kilometer starting in Bordeaux (at the Stone Bridge) as KP 1 and ending at the mouth of the estuary at KP 100. For each year, the number of *A. sturio* caught is indicated as N=.

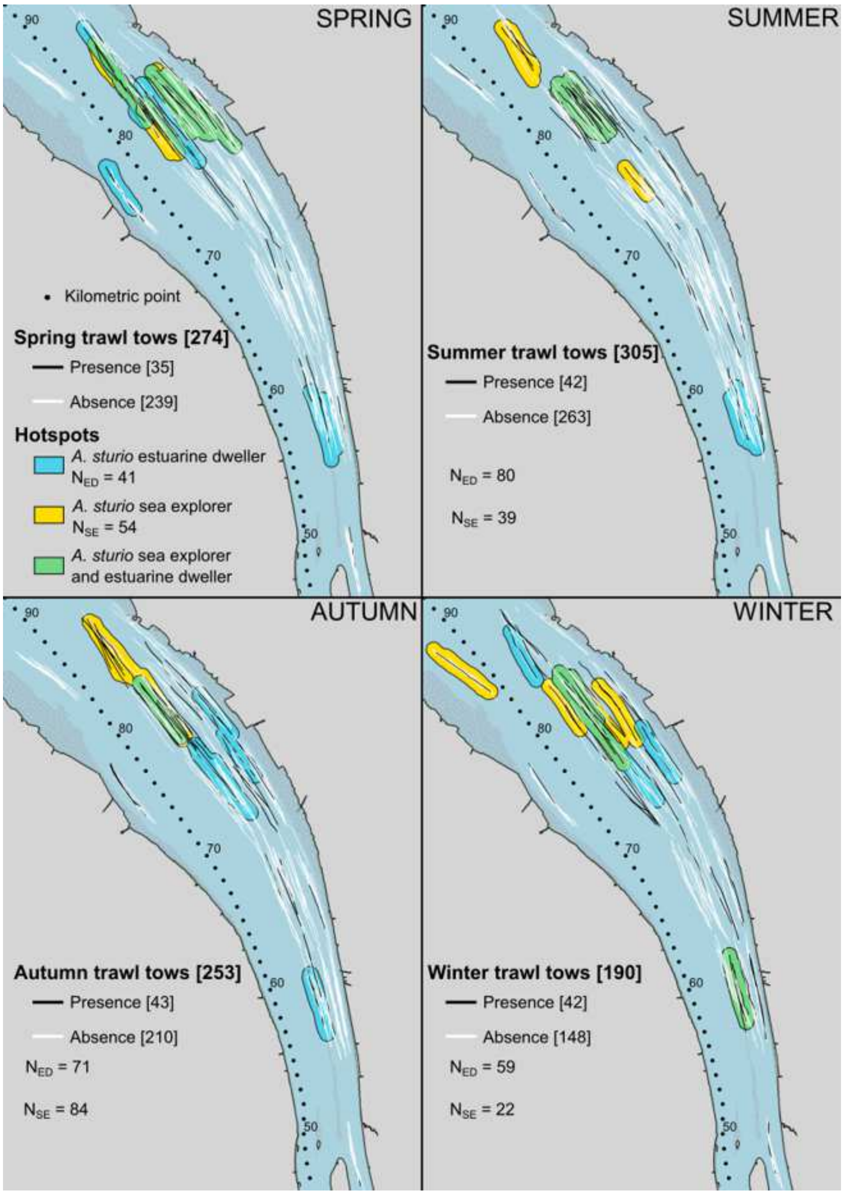


Figure with colours

Figure 5: spatial representation of the trawl tows and of the hotspots at the seasonal scale for the 2010-2018 sampling period.

The numbers of trawl tows are indicated [] as well as the number of *A. sturio* per group N_{ED} = and N_{SE} =.

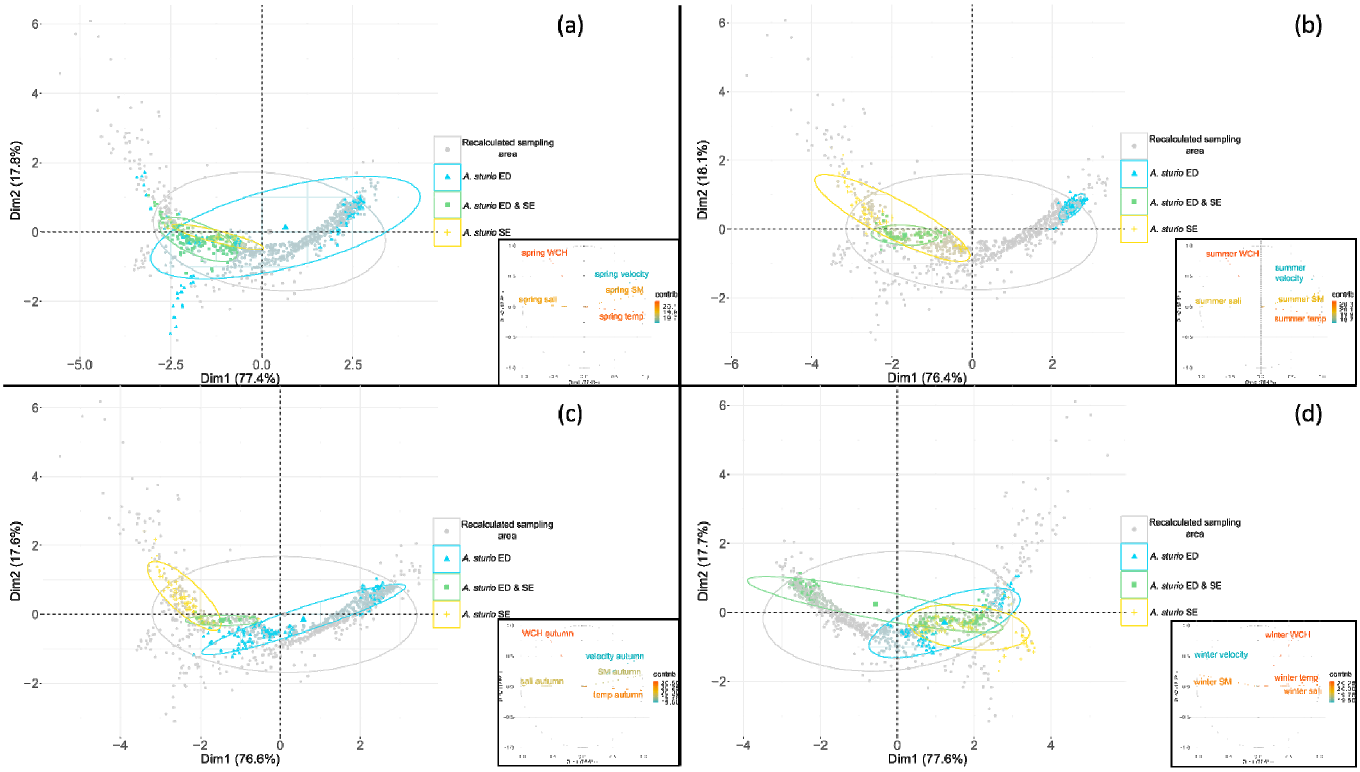


Figure with colours

Figure 6: Representation of the Principal Component Analysis results for each season.

(a) Spring; (b) Summer; (c) Autumn; (d) Winter. ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

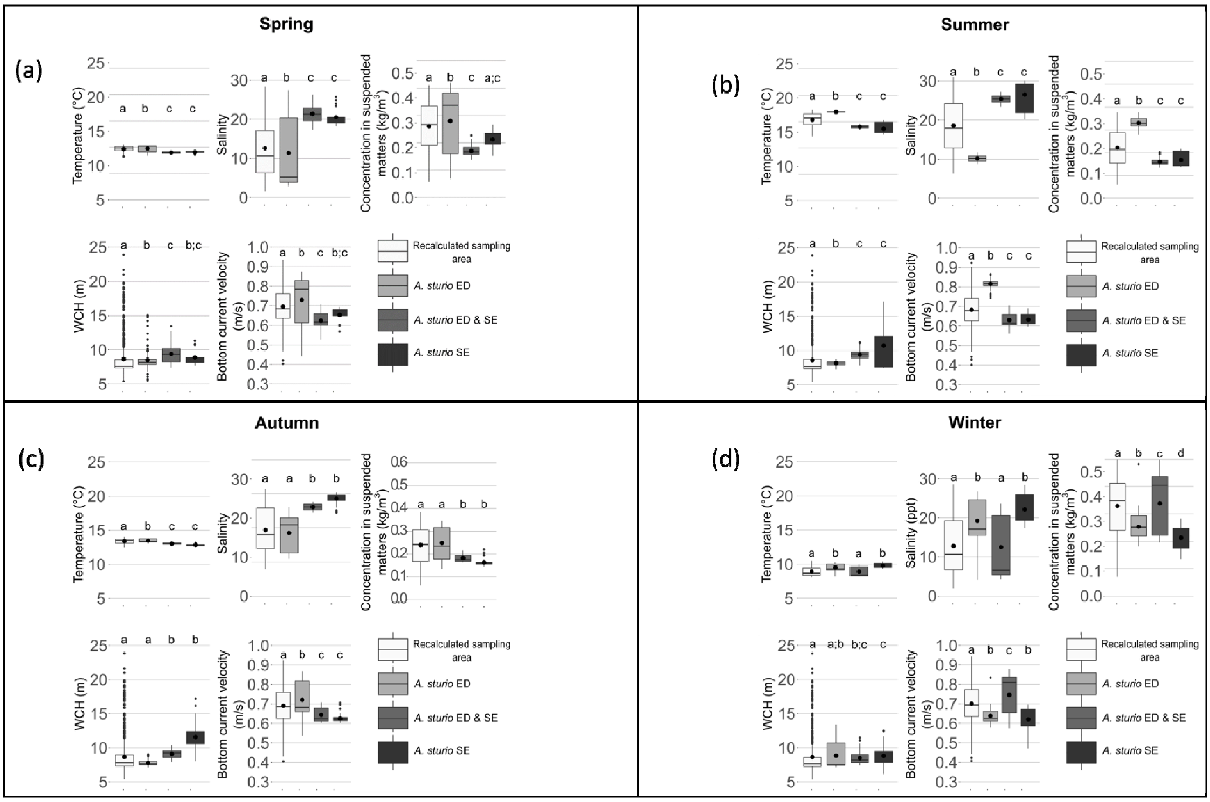
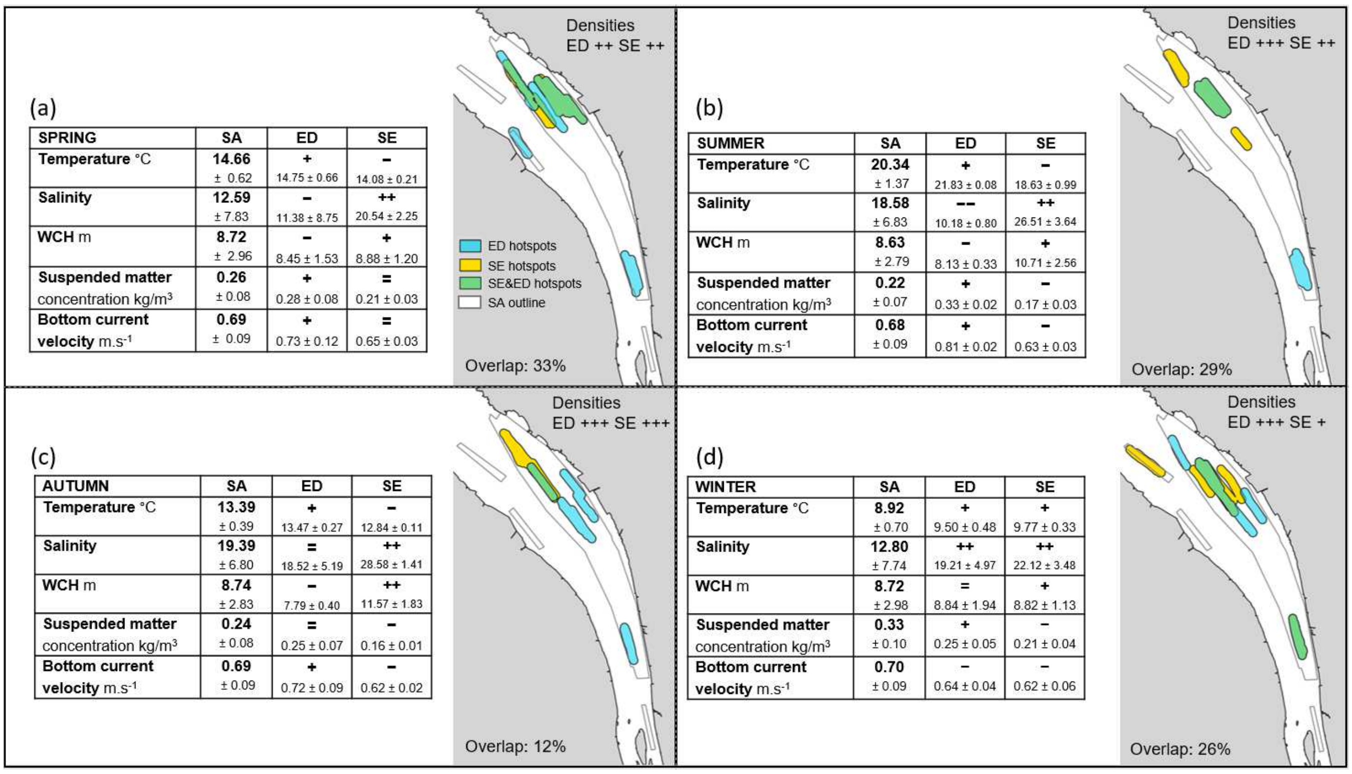


Figure 7: Boxplots of the modelled environmental variables corresponding to the hotspots of the different size groups and of the recalculated sampling area per season.

ED stands for Estuarine Dwellers and SE stands for Sea Explorers.



(a)

SPRING	SA	ED	SE
Temperature °C	**14.66** ± 0.62	+ 14.75 ± 0.66	− 14.08 ± 0.21
Salinity	**12.59** ± 7.83	− 11.38 ± 8.75	++ 20.54 ± 2.25
WCH m	**8.72** ± 2.96	− 8.45 ± 1.53	+ 8.88 ± 1.20
Suspended matter concentration kg/m^3	**0.26** ± 0.08	+ 0.28 ± 0.08	= 0.21 ± 0.03
Bottom current velocity m.s^{-1}	**0.69** ± 0.09	+ 0.73 ± 0.12	= 0.65 ± 0.03

(b)

SUMMER	SA	ED	SE
Temperature °C	**20.34** ± 1.37	+ 21.83 ± 0.08	− 18.63 ± 0.99
Salinity	**18.58** ± 6.83	−− 10.18 ± 0.80	++ 26.51 ± 3.64
WCH m	**8.63** ± 2.79	− 8.13 ± 0.33	+ 10.71 ± 2.56
Suspended matter concentration kg/m^3	**0.22** ± 0.07	+ 0.33 ± 0.02	− 0.17 ± 0.03
Bottom current velocity m.s^{-1}	**0.68** ± 0.09	+ 0.81 ± 0.02	− 0.63 ± 0.03

(c)

AUTUMN	SA	ED	SE
Temperature °C	**13.39** ± 0.39	+ 13.47 ± 0.27	− 12.84 ± 0.11
Salinity	**19.39** ± 6.80	= 18.52 ± 5.19	++ 28.58 ± 1.41
WCH m	**8.74** ± 2.83	− 7.79 ± 0.40	++ 11.57 ± 1.83
Suspended matter concentration kg/m^3	**0.24** ± 0.08	= 0.25 ± 0.07	− 0.16 ± 0.01
Bottom current velocity m.s^{-1}	**0.69** ± 0.09	+ 0.72 ± 0.09	− 0.62 ± 0.02

(d)

WINTER	SA	ED	SE
Temperature °C	**8.92** ± 0.70	+ 9.50 ± 0.48	+ 9.77 ± 0.33
Salinity	**12.80** ± 7.74	++ 19.21 ± 4.97	++ 22.12 ± 3.48
WCH m	**8.72** ± 2.98	= 8.84 ± 1.94	+ 8.82 ± 1.13
Suspended matter concentration kg/m^3	**0.33** ± 0.10	+ 0.25 ± 0.05	− 0.21 ± 0.04
Bottom current velocity m.s^{-1}	**0.70** ± 0.09	− 0.64 ± 0.04	− 0.62 ± 0.06

Figure with colours

Figure 8: Summary diagram of the main results per season.

(a) stands for spring, (b) stands for summer, (c) stands for autumn and (d) stands for winter.

SA stands for recalculated sampling area; ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

For each modelled environmental variables the mean and the standard deviation are indicated in the tables.

In the ED and SE column, the sign = (similar), + (above) or – (below) are set compared to the SA.

For the densities the numbers of + are relative to the seasons considered.

		Spring	Summer	Autumn	Winter
Test	Pairs	p-value			
NPMANOVA		***			
Pairwise adonis	SA – SE	***	***	***	***
	SA – ED	0.618	***	0.192	***
	SA – ED & SE	***	***	***	0.702
	SE – ED	***	***	***	***
	SE – ED & SE	0.738	*	***	***
	ED – ED & SE	***	***	***	***

Table 1: Results of the NPMANOVA and the associated post-hoc test per seasons.
*** means p-value < 0.001; * means p-value < 0.05. SA stands for recalculaed sampling area; ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

Tables in supplementary material

Spring		**Salinity**	**Temperature**	**WCH**	**SM**	**Velocity**
Dunn test	SA – ED	*	***	***	*	**
	SA – ED & SE	***	***	***	***	***
	ED – ED & SE	***	***	***	***	***
	SA – SE	***	***	***	0.06	0.09
	ED – SE	***	***	0.29	*	**
	SE – ED & SE	0.65	0.66	0.45	0.06	0.10

Table 1: Dunn test for spring.
*** means p-value < 0.001; ** means p-value < 0.01; * means p-value < 0.05. ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

Summer		**Salinity**	**Temperature**	**WCH**	**SM**	**Velocity**
Dunn test	SA – ED	***	***	**	***	***
	SA – ED & SE	***	***	***	***	***
	ED – ED & SE	***	***	***	***	***
	SA – SE	***	***	***	***	***
	ED – SE	***	***	**	***	***
	SE – ED & SE	0.41	0.36	0.55	0.71	0.95

Table 2: Dunn test for summer.

*** means p-value < 0.001; ** means p-value < 0.01; * means p-value < 0.05. ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

Autumn		**Salinity**	**Temperature**	**WCH**	**SM**	**Velocity**
Dunn test	SA – ED	0.07	*	0.06	0.15	**
	SA – ED & SE	***	***	***	***	**
	ED – ED & SE	***	***	***	***	***
	SA – SE	***	***	***	***	***
	ED – SE	***	***	***	***	***
	SE – ED & SE	0.08	0.07	0.05	0.14	0.21

Table 3: Dunn test for autumn.

*** means p-value < 0.001; ** means p-value < 0.01; * means p-value < 0.05. ED stands for Estuarine Dwellers and SE stands for Sea Explorers.

Winter		**Salinity**	**Temperature**	**WCH**	**SM**	**Velocity**
Dunn test	SA – ED	***	***	0.19	***	***
	SA – ED & SE	0.39	0.52	***	*	***
	ED – ED & SE	***	***	0.05	***	***
	SA – SE	***	***	***	***	***
	ED – SE	0.06	0.07	*	*	0.56
	SE – ED & SE	***	***	0.43	***	***

Table 4: Dunn test for winter.
*** means p-value < 0.001; ** means p-value < 0.01; * means p-value < 0.05. ED stands for Estuarine Dwellers and SE stands for Sea Explorers.