A QUANTILE REGRESSION APPROACH TO DEFINE OPTIMAL ECOLOGICAL NICHE (HABITAT SUITABILITY) OF COCKLE POPULATIONS (CERASTODERMA EDULE)

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Abstract

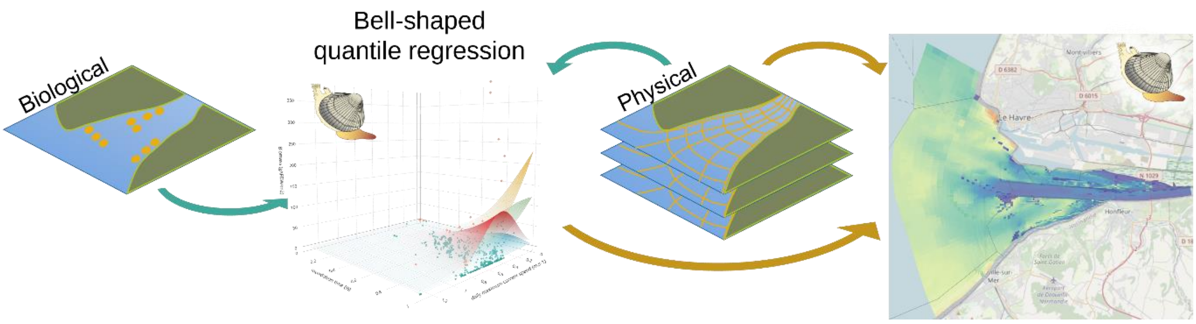
For several decades now, species distribution models (SDMs) have been a promising area of ecological research. The aim of the present study is to define optimal ecological niches and habitat suitability for the population of the bivalve *Cerastoderma edule* in the Seine estuary. The method involved applying quantile regression to a 20-year biological dataset at the scale of the estuary, coupled with a hydro-morpho-sedimentary model data set validated over a longer period (25 years) also at the scale of the estuary, using 100-m mesh cells. This study was carried out to describe biological responses to environmental factors involved in defining an optimal ecological niche, using the bifactorial Gaussian equation using physical forcings (tidal currents, bed shear stress, etc.) as explanatory factors. On the basis of a preliminary multivariate analysis of the physical descriptors, a comparison was made between three different types of equation (linear, B-spline and Gaussian) in four sets of paired environmental factors: daily maximum current speed & inundation time, daily salinity range & temperature, daily salinity range & bathymetry, daily maximum bed shear stress & mud content. The non-linear quantile regression with a bifactorial Gaussian equation produced the best description of habitat suitability and optimal niches, at the 95th centile and using the biomass (gAFDW/m² - Ash Free Dry weight). Daily maximum current speed & inundation time and daily salinity range & temperature were the most pertinent SDMs. The optimal ecological niche for *C. edule* appeared to be lower intertidal marine areas, with temperate and low dynamic waters, settled in muddy sand sediment of the tidal flats of Seine estuary. Using this technique, the calculation of optimal niches in this ecosystem was explored over a period of 25 years and analysed in isolated sectors and can now be applied in different scenarios related to the global

warming. We propose several reliable models, so that different kinds of prediction can now be applied according to the context of future scenarios.

Highlights

- Bifactorial gaussian quantile regression, with a high quantile, e.g. the 95th centile, is performant to express the optimal ecological niche of *C. edule* at the scale of the estuary.
- Daily maximum current speed and inundation time are the most adequate factors to describe the estuary, thus to build an SDM.
- Suitability index was built based on optimal ecological niches to assess habitability of areas in the Seine estuary.
- Optimal *Cerastoderma edule* conditions correspond to low intertidal marine shores, temperate and moderate currents in muddy sand sediment.

Graphical abstract



Keywords

Cerastoderma edule, quantile regression, species distribution model, optimum ecological niches, habitat suitability

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1 Introduction

Understanding the links and interactions between abiotic and biotic components is necessary to preserve and restore areas affected by environmental fluctuations caused by human activity, and to conserve the benefits of their ecosystem services (Richards and Lavorel, 2023). The concept of ecological niches was defined to better understand and predict the population dynamics (Hutchinson, 1957). Hutchinson conceptualised an ecological niche as "the n-dimensional set of environmental conditions that allow a species to live and reproduce".

A species distribution model (SDM) is an approach providing practical information on the spatial distribution of species based on ecological niche modelling. The construction of an SDM requires the definition and selection of three main components: 1) an ecological model that brings context to the way the SDM will be produced and analysed; 2) a data model defining how the data are collected and prepared; 3) a statistical model involving the choice of statistical method, error function and significance tests (Austin, 2007, 2002).

A wide choice of statistical models for constructing SDM is available, with two main categories: the correlative ones (Austin, 2002; Guisan and Zimmermann, 2000) and the mechanistic ones (Kearney and Porter, 2009). Each approach has advantages and disadvantages (Kearney and Porter, 2009; Melo-Merino et al., 2020), but the vast majority of studies carried out to date are correlative (Robinson et al., 2011). Correlative SDMs link the presence or abundance of a species with spatial habitat data, thereby quantifying the relation between environmental factors and species distributions. The model define an environmental profile on an empirical basis, making it possible to define the abiotic factors determining the maintenance of a species and to infer its presence or absence in areas where no biological data are available, or the impact of changing abiotic conditions (Elith and Leathwick, 2009; Franklin, 2010; Guisan and Thuiller, 2005). These methods generally use geolocalised biological data of a species and abiotic parameters measured by techniques such as field or remote measurements or modelling (Brown et al., 1996; Guisan and Zimmermann, 2000; Melo-Merino et al., 2020; Van Der Wal et al., 2008).

Various and increasing statistical tools can be used with correlative SDMs, among them the regressions are often based on either Ordinary Least Square (OLS) or Generalized Linear Models (GLMs, fitted by Maximum Likelihood Estimation), which describe the distribution of biological response with the chosen abiotic predictors (Bolker et al., 2009; Robinson et al., 2017). These approaches provide access to a level of information that is rather complex to interpret, given the patchy spatial distribution of many species, variations in recruitment from one year to the next, and the complex life cycles of some species (Ysebaert and Herman, 2002). In particular, the construction of a SDM based on several abiotic measurements cannot account for other factors, either because they are not available or are not known. Those factors may have a limiting effect on the biological response which will then reflect the response to these unknown limiting factors. This is the statement of Liebig's law of minima: if other resources are not optimal for certain observations, the measured response of the species will be less than the maximum possible response to the observed resource. As a result, OLS or GLM models incorporate the effects of unmeasured limiting factors on the SDM (Austin, 2007; Cade et al., 1999).

Quantile regression (QR) is defined as a sequence of ascending envelopes that cover an increasing proportion of occurrence according to quantiles (Koenker and Hallock, 2000; Koenker and Machado, 1999). Studies have been conducted for more than 40 years to carry out QR, and recent advances in computer tools have improved its use, refined the performance indicators, and facilitated its interpretation especially for ecological applications, such as SDM (Austin, 2007; Cade et al., 2005, 1999; Cade and Noon, 2003). When the time scale is long, we can admit that there is one real probability that the population express its maximum response at a moment (“when all planets are aligned”). By targeting the upper quantiles of the distribution in long-term surveys, it is possible to define the best maximum biological response to abiotic predictors, with any other factors, whether biological, environmental or mobility, that are not accounted for, being considered as non-limiting (Schröder et al., 2005). The use of QR in a correlative SDM with a sufficiently rich database and over a sufficiently long period of time, makes it possible to define the optimal conditions for a species with respect to selected abiotic factors, freeing it from particular recorded conditions (meteorological conditions, sanitary events, lifespans). In addition, the effects of interaction between species, with their environment and the biogeochemical processes they generate can make environments more dynamic and welcoming on a very local scale, through a system of self-organisation. This can lead to very high densities of a species in a local 'patch', a phenomenon often observed in estuarine environments. Thrush modelled species distributions based on the maximum density of intertidal species (Thrush et al., 2003). Quantile regression follows the same principle, but is less 'optimistic', because it is unlikely that the extreme densities measured at a very local level can be extended to larger scales with the same amplitude. In other words, the variability observed below the upper quantiles is related to factors that are not observed and above the upper quantiles reflects the auto-organisation processes of biological populations (Weerman et al., 2011, 2010). In this way, a correlative SDM with QR get close to the main impacts of abiotic factors on the biological response, thus defining the optimal ecological niche. What is more, using abundance or biomass as the biological response, one obtains more than a specific geographical range based on presence/absence. Biomass is rather related to the growth and aging ability of individuals, whereas density rather indicates the patchiness of distribution and the effect of recruitment. Both are consequently meaningful to study how long a population live.

Considerable work has been invested in SDM for many years, but only recently included marine environments, and the focus was more on pelagic areas (Melo-Merino et al., 2020; Robinson et al., 2011, 2017), whereas intertidal and estuarine areas were less studied. Brown et al. mentioned the importance of ecological gradients (Brown et al., 1996), estuarine and intertidal environments are undeniably subject to massive, repeated and frequent gradients, due to the action of the tide and the influence of the river, both of which have major impacts on abiotic factors. However, the challenges of managing estuaries and coasts in the context of climate change and anthropogenic pressure are key issues (Crossland et al., 2005; Grassle, 2013). With respect to ecosystem services, among other things, an estuary is a shipping lane, a fishing ground and an area comprising diverse natural habitats. All these activities compete for space and have different needs and yet are linked to each other, so there is a need for decision support tools that improve their management and foresee their future development (Degraer et al., 2008; He et al., 2015; Schickele et al., 2020). The vulnerability of estuarine sediments to the sea level increase is studied for a long time (Healy et al., 2002) and it is very relevant to focus on the response of the benthic macrozoobenthos not only to temperature or salinity changes, but also to physical dynamics (current velocity, bed shear stress, sediment composition).

In estuarine ecosystems, benthic macrofauna (or macrozoobenthos) is found at different levels depending on the trophic guild to which it belongs (Dubois et al., 2007; Saint-Béat et al., 2013). The capacity of benthic macrofauna to resist external stressors is yet not fully understood, but abiotic factors are habitat-defining parameters on which a cohort of species depends (Ysebaert and Herman, 2002). In particular, sediment and hydrological parameters have a direct impact on the activity and spatial distribution of macrozoobenthos, with sediment acting as a food source, habitat, shelter and breeding ground but which can also cause discomfort. Sediment indicators, including grain size median and fine silt content, have been shown to strongly contribute to explaining variations in macrozoobenthic communities (Anderson, 2008; Thrush et al., 2005, 2003). The benthic macrofauna of the Seine Bay (Normandy, France) has been extensively studied in recent decades (Bacouillard et al., 2020; Baffreau et al., 2017; Dauvin, 2015; Le Guen et al., 2019) and estuarine management included in subsequent regional program frameworks (https://www.seine-aval.fr/). Accessing abiotic factors, and especially physical forcings, in an estuary is a challenge that can be solved by developing hydro-morpho-sedimentary (HMS) models, which use principles of fluid and particle physics to define the parameters of interest in the estuary at an intermediate scale. The Seine estuary (Normandy, France) was the subject of the Mars3D model adjustment, which describes the dynamics of the physical parameters in an estuary, such as bottom elevation, salinity, temperature, current velocity, water surface elevation, with a particular effort invested in describing the erosion, deposition and consolidation properties of sand-mud mixtures (Grasso et al., 2021, 2018; Grasso and Le Hir, 2019; Mengual et al., 2020; Schulz et al., 2018). Such tools allow a temporal projection at a regional spatial scale and hence to make projections based on different sets.

In a similar intertidal environment, examples of correlative SDMs using QR were developed by (Cozzoli et al., 2017, 2014, 2013). Indeed, using a long series of benthic macrofauna sampling campaigns in the Oosterschelde estuary (The Netherlands), and an HMS model in the same area, the SDM with QR above the 90th percentile enabled identification of the optimal conditions for biological response, in this case biomass, according to annual averages of the chosen factors. The authors characterize this model as habitat suitability or potential niche. By modelling a type of habitat rather than a biological response, this type of model reduces inter-annual variations caused by many unmeasured factors, is more informative about the environment under study, and provides a more functional management guide. Habitat suitability, i.e., relationships that describe physical-biological coupling, can then be used to understand the long-term and large-scale evolution of benthic species in response to changes in abiotic conditions, whether natural, anthropogenic, or due to climate change.

In practice, correlative SDM with QR does not presuppose the type of equation that links abiotic factors to a biological response, or even the number of predictors to be used. This method can be used together with an expected response curve for each factor. It was observed that the biological response to physical factor is often non-linear, and can be modelled by a Gaussian distribution (Huisman et al., 1993; Van Der Wal et al., 2008). In the present study, we built a SDM for an optimal ecological niche, to analyse the links between the spatial distribution of species and the physical characteristics of their habitat. The model consists in a correlative SDM based on QR (the statistical model) that provides a spatial description of the gradient of the best biological response (maximal occurrence) in regard of selected abiotic factors generated by a hydro-morpho-sedimentary model. Using the *Cerastoderma edule*, the common cockle, as an example, the study compares the performances and results of linear, Gaussian and B-spline QR models as ecological models. Several combinations of abiotic factors were chosen because as mentioned in (Guisan and Zimmermann, 2000) “Nature is too complex and heterogeneous to be predicted accurately in every aspect of time and space from a single, although complex, model”. After applying a multivariate analysis (PCA) on physical descriptors, four sets based on combinations of two abiotic factors were processed because they can answer different ecological questions: daily maximum current speed & inundation time, daily salinity range & water temperature, daily salinity range & bathymetry, daily maximum bed shear stress & mud content. These models were geographically applied and analysed. A suitability index is also proposed as a tool for the management of estuarine ecological areas.

2 Materials and Methods

All data processing was conducted in R version 4.2.2 (2022-10-31 ucrt) except for Mars3D pre-treatment in Matlab 2019a. Significance levels are $p < .0001$ with “****”, $p < .001$ with “***”, $p < .01$ with “**”, $p < .05$ with “*”.

2.1 Study area

The Seine estuary in Normandy, north-western France, is defined as the last 170 km of the river leading to the marine ecosystem close to Le Havre, it starts at Poses weir upstream and ends in the Seine Bay downstream. The Seine estuary is macrotidal (tidal range up to 8 m), and is subject to fresh water inflows ranging from 100 to more than 1000 $m^3.s^{-1}$, with a mean of 450 $m^3.s^{-1}$ in the two last decades. Tidal dynamics and the wave regime have a significant impact on the hydro-sedimentary dynamics of the mouth of the estuary (Grasso et al., 2021; Schulz et al., 2018).

The mouth of the estuary hosts a variety of habitats that provide many ecosystem services (Beck et al., 2001; Boesch and Turner, 1984). In particular, intertidal mudflats play a crucial role in the Seine estuary and are areas of major interest including for nutrient recycling, coastline protection and as feeding / nesting sites for migratory birds. The Seine estuary is marked by structures that have profoundly modified this ecosystem, which is still undergoing changes that began at the beginning of the 20th century (Lesourd et al., 2016). Numerous dykes have been built and dredging has been carried out to increase the capacity of the navigation channel, which contributed to the disconnection of the two banks of the estuary and reduced the extent of wetlands. Among these works, some were huge projects construction of Normandy Bridge (1989-1995), which crosses the Seine estuary and the “Port 2000” project (2000-2005) to enlarge the port of Le Havre, mainly to allow large container ships to access new all-day loading platforms.

The Port 2000 project involved ecological compensation in the form of the creation of a nature reserve in 1997, as well as the digging and dredging of an artificial channel in the north upstream mudflat and the creation of a small island (Ilot Oiseaux) for migratory birds in the southern mudflat (Aulert et al., 2009). Several historically known areas in the Seine estuary that differ in either their habitat or community have been studied, mainly mudflats and subtidal areas (Morelle et al., 2020; Tecchio et al., 2016) (Figure 1).

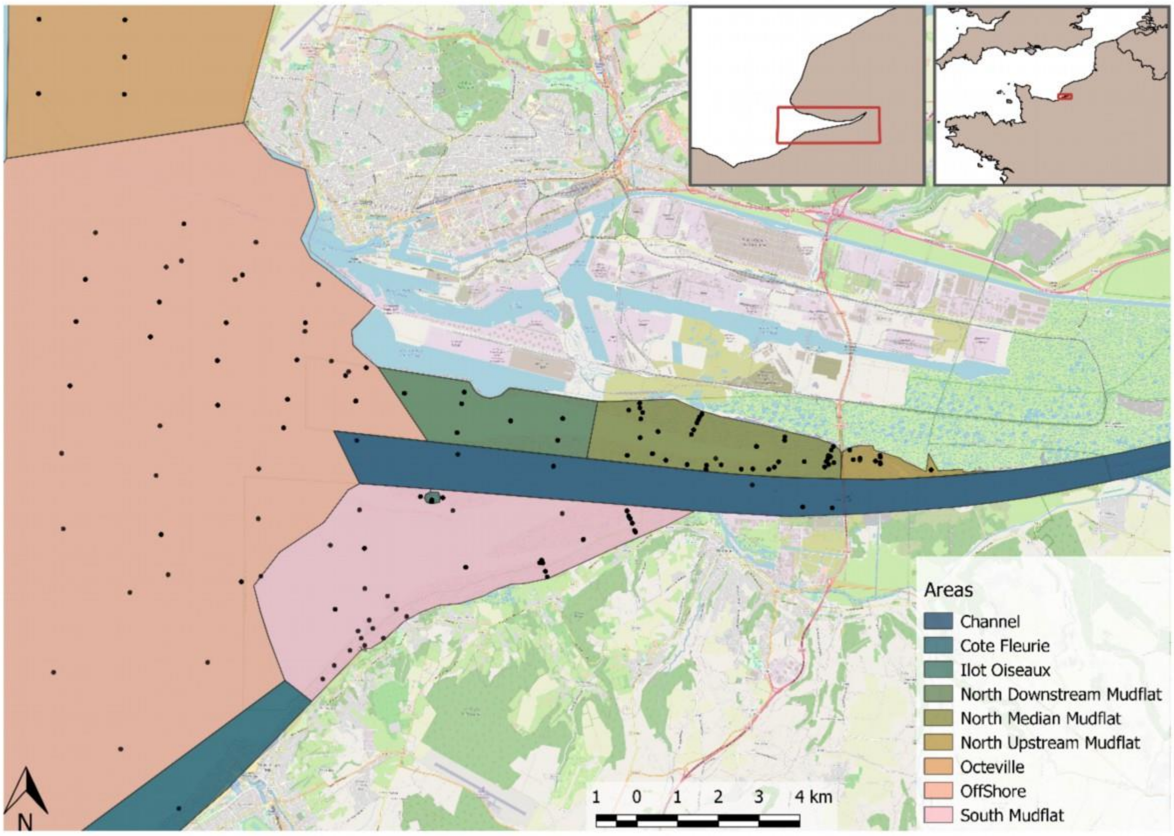

Figure 1 Maps showing the habitats defined in the dataset of the study area. Dots represent the location of the biological samples.

2.2 Biological model

The cockle *Cerastoderma edule* (Linnaeus, 1758) is a bivalve belonging to the family of Cardiidae which is widely distributed and exploited in waters off northern Europe up to north Iceland and off the coast of West Africa down to southern Senegal (Hayward and Ryland, 1995). The oval ribbed shells of the cockle can reach 6 cm in diameter and are white, yellowish or brown in colour, and its lifespan is 2-3 years (Malham et al., 2012). Cockles are suspension-feeders, inhabiting the few uppermost centimetres of the sediment with its two siphons emerging from the surface. Its growth depends mainly on microphytobenthos in the juvenile stage and on trophic phytoplankton in the adult stage (Sauriau and Kang, 2000).

Cockle habitats are located in the central areas of the foreshore subject to medium currents (between 0.3 and 0.7 $m.s^{-1}$ of maximum tidal current speed) (Herman et al., 1999; Ysebaert et al., 2002), typical marine salinity (> 30) and they prefer fine sands (slightly silty, grain size between 100 and 200 µm) (Cozzoli et al., 2014; Ubertini et al., 2012). This species can be found at particularly high densities in the English Channel, the most densely inhabited area being the Bay of Veys, (density in the order of 200 to

500 ind.m-²), and may exceptionally exceed 5000 ind.m^{-2} (Gosling, 2003; Mahony et al., 2022). Winter conditions, current intensity and stress (erosion) appear to explain the high mortality rates observed in some years (Herman et al., 1999; Van Colen et al., 2010).

2.3 Datasets

2.3.1 Biological data

Data concerning the benthic macrofauna of the Seine Bay are grouped in a database named *MAcrobenthos Baie et Estuaire de Seine* (MABES) (Dauvin et al., 2006; L'Ebrellec et al., 2019). This dataset provides information on sampling (geolocation, sampling method) and fauna (density [ind.m^{-2}], biomass [gAFDW.m^{-2}] – Ash Free Dry Weight) collected in several projects for the past 40 years. This database was completed with data from the *Cellule de Suivi du Littoral Normand* (CSLN) surveys conducted for the *Maison de l'Estuaire*.

The raw data (n = 50,948) were harmonised and grouped in a single database which contain a total of 31,079 observations, and 187 sampling stations (with some variation in coordinates from year to year), with an average of 87 stations sampled in each campaign (depending of the project), mainly in September, October, and November. A series of 5-year periods was chosen among the periods covered by the dataset, from 2000 to 2019 (the years before 2000 were discarded as they contained too few observations, n = 216), with only one or two sampling campaigns per year: 2000-2005, including the construction of 'Port 2000' which caused major disruptions in the estuary; 2006-2010; 2011-2015; 2016-2019. A total of 627 different species are contained in the records.

2.3.2 Hydro-Morpho-Sedimentary data

The HMS dataset was generated during the ARES project using the Mars3D model (Grasso et al., 2021, 2019). Mars3D can be used in the context of estuarine hydrodynamics and application to fine sediment and sand transport. This three-dimensional (3D) process-based model was set up and run under realistic forcings (including tide, waves, wind, and river discharge). The Mars3D model is composed of the hydrodynamic core forced by the WAVEWATCHIII® wave model (Roland and Ardhuin, 2014) coupled with the MUSTANG sediment module (erosion, deposition, consolidation…). MUSTANG accounts for spatial and temporal variations in sand and mud content in the multi-layer sediment bed, as well as for consolidation processes, and also resolves advection/diffusion equations for different classes of particles in the water column (Grasso et al., 2018; Le Hir et al., 2011; Mengual et al., 2020).

The ARES dataset covers the simulation periods 1990-2000 and 2005-2018. The period 2001-2004 was not modelled because it corresponds to the period of construction of the Port 2000 project. The dataset outputs are available at intervals of 30 minutes for the entire Seine Bay area each hydrological year, starting on October 1st and finishing on September 30th. The hydrological sub-data contain 58 variables, some of which depend on water depth, with 10 levels in the water column, of which only the median of the 3 lower layers were retained to reflect benthic conditions: current speed, temperature, salinity and SPM for 5 particles sizes. The other variables retained are bathymetry and the inundation rate calculated from bathymetry and water height. The sedimentary sub-data contain 19 variables, some of which depend on the depth in the sediment, with 6 levels corresponding to 1 m, of which only the median of the 4 upper layers is retained, i.e. 10 cm to reflect benthic conditions: temperature, salinity and sediment concentration for 5 particles sizes. The other variables retained are the total thickness of the sediment and the bed shear stress.

In addition to these variables, processing was carried out to extract other information. The daily maximum was calculated for current speed and bed shear stress, the daily range was calculated for salinity and temperature, and the yearly sediment budget was calculated from the variation in sediment thickness at the beginning and end of the year. The sediment total concentration is the sum of all sediment concentrations, and the mud content was deduced from the different particle size concentrations. All the variables selected and created, 14 in all, were brought down to a median calculated over the hydrological year.

The 14 abiotic factors were studied to select the most relevant factors and limit their number to avoid autocorrelations. A PCA (`FactoMineR::PCA` and `factoextra` package for visualisation) based on a correlation matrix was carried out on all the factors, allowing complementary parameters to be identified on the two main axes. In addition, a correlation matrix provides a complementary view of the dataset, including the biomass and density of *C. edule* to ensure that there is no direct correlation between abiotic and biotic factors. Based on those analyses, 4 couples of abiotic factors were chosen.

2.4 Model adjustments

2.4.1 Quantile regression

The quantile regression (QR) mathematical theory has been extensively expanded and described by Koenker in recent decades (Koenker, 2019; Koenker et al., 2019; Koenker and Bassett, 1978; Koenker and Hallock, 2000, 2001; Koenker and Machado, 1999). Its use in ecological studies has increased significantly since the work of Cade and Noon (Cade et al., 2005, 1999; Cade and Noon, 2003).

Three different types of models were defined in this study (Table 1), all using two abiotic factors, but with different functions to link them to the biological response. Mathematical notation is based on (1) the τ subscript for variables that are quantile-dependent, (2) β for model coefficients, that are vectors of length τ, (3) μ and σ for mean and standard deviation. QR were performed with the *quantreg* package in R developed by Koenker. The three model types were computed with different quantiles τ = [0.5, 0.9, 0.95, 0.975], 0.5 being the equivalent of an OLS regression, and kept as a reference, the other values higher than 0.9 to seek for the optimum response.

The model was adjusted on the biological data with an associated HMS cell to create SDMs, which were then applied to the HMS data set, focused on the estuary. The maximum of the SDM niche response was used to normalize the model response, to create a suitability index, ranging from 0 to 1.

Table 1 List of types of models tested

Name	Type	Equation	Rationale
RQ2int	RQ linear with interaction	$y_\tau = \beta_{0\tau} + \beta_{1\tau}.x_1 + \beta_{2\tau}.x_2 + \beta_{3\tau}.x_1.x_2$ `quantreg::rq(x1*x2)`	Comparison with the results in (Cozzoli et al., 2014)
RQ2nli	RQ bifactorial gaussian (non-linear)	$y_\tau = \mathrm{A}.e^{-\left[\frac{(x1-\mu1_\tau)^2}{2.\sigma2_\tau^2}+\frac{(x2-\mu2_\tau)^2}{2.\sigma1_\tau^2}\right]}$ `quantreg::nlrq(f(x1,x2, initial.conditions))`	With μ and σ initiated by the mean and the standard deviation for each predictor (Huisman et al., 1993; Schröder et al., 2005).
RQ2bsp	RQ linear with B-Spline	`quantreg::rq(splines::bs(x1,degree=3,knots=median(x1))*bs(x2,degree=3,knots=median(x2)))`	Avoid pre-determined shape of the equation and the use of a non-linear function (Cozzoli et al., 2013)

2.4.2 Model selection

QR model validation was based on the Akaike Information Criterion (AIC). This index evaluates the performance of the model using the fewest possible predictors (Akaike, 1974), and was adapted to the QR (Cade et al., 2005), named AICc, and the delta with the minimum of the model series was processed (ΔAICc). Following Koenker's recommendation, the R^1, equivalent to OLS R^2 developed by Koenker and Machado (Koenker and Machado, 1999), was not used (Koenker, 2006).

In addition to AICc, the relationship between predicted and observed values was plotted. The predicted (model output) data were discretized in 10 homogeneous classes and for each class, the corresponding sample quantile of the observed data was calculated, with a bootstrap (R=1000) to cope with the limited number of records. To assess the validity of the model, a linear correlation was drawn for each quantile.

3 Results

High resolution and interactive figures are in the supplementary data in https://am-lh.github.io/Melting_pot/SDM/SDM_Suppl_Data.html.

3.1 Description of the biological data set

Biological data for *C. edule* comprised a total of n = 543 observations. The observations were split into periods: 2000-2005 (n = 108), 2006-2010 (n = 155), 2011-2015 (n = 174), 2015-2019 (n = 106). The following treatment focussed on the mudflats used by *C. edule* (south mudflat (n = 218), north median mudflat (n = 198), north downstream mudflat (n = 82), north upstream mudflat (n = 2)). Differences in biomass and density are detailed as a function of the period and the different areas concerned (Supp. Data 3.1). The only noticeable spatial and temporal differences concerned biomass in the south mudflat and the north (median and downstream) mudflats in the period 2000-2005.

3.2 Selection of the Hydro-Morpho-Sedimentary factors and their association

The PCA analysis on physical descriptors (Figure 2, Supp Data 3.2, detailed scores Table 2) gives 3 main dimensions for a total variance of 65.4 % (PC1 = 28.8 %, PC2 = 20.7 %, PC3 = 15.9 %):

- PC1 corresponds to the hydrodynamics of the area with the contributions of: daily maximum current speed (19.6 %), current speed (17.8 %), daily salinity range (17.8 %), daily maximum bed shear stress (10.9 %), MES mud (9.2 %), bed shear stress (8.7 %).
- PC2 is related to the morphology of the estuary: inundation time (23.1 %), daily temperature range (20.4 %), bathymetry (19.9 %), salinity (14 %), temperature (8.3 %).
- PC3 describes the sediments characteristics of the bed: sediment total concentration (30.2 %), mud content (29 %), bed shear stress (18 %), daily maximum bed shear stress (7.2 %).

Considering those axes, sets were built with two abiotic factors from different axis to more accurately describe the environment. The sets tested were:

A. Daily maximum current speed [$m.s^{-1}$] & inundation time [%] – PC1-PC2: These variables are the main contributors of the two firsts axes, are easily retrieved at high frequency and enable comparison with the study by Cozzoli et al. (Cozzoli et al., 2014). They are also interesting because they contain information on the localisation of the tidal area that could evolve with sea level rise and information on the hydrological conditions including fluctuations in the flow rate of the river linked to climate change. A significant correlation was observed between these two variables in the HMS dataset (R^2 = 0.56****).

B. Daily salinity range & temperature [°C] – PC1-PC2: These factors are easily measurable at high frequency (Goberville et al., 2010) and are not correlated (R^2 = 0.02 ns). They illustrate two aspects of climate change: changes in the river regime which have an impact on the salinity profile of the estuary (Lheureux et al., 2022), and variations in water temperature (globally increase), to which species must gradually adapt. Daily temperature range, which made a better contribution to the PCA than temperature, provides information on the tidal thermal stress suffered by fauna. However, it is strongly defined by bathymetry, thus would reflect the sea level rise rather than long-term changes of temperature, it was therefore not selected.

C. Daily salinity range & bathymetry [m] – PC1-PC2: Both factors are accessible at high frequency, at large scale, and can be measured remotely. They provide a good geographical description of the estuary, and are strongly affected by climate change, especially by the global sea level rise, marine intrusion, and changes in the river regime. They are not significantly correlated (R^2 = -0.08 ns).

D. Daily maximum bed shear stress [Pa] & mud content [%] – PC1-PC3: These variables play a determining role in building an erosion model in the HMS model (R^2 = -0.29****). In addition, the choice relies on close links between the features of the sediment and the responses of the benthic communities (Andersen et al., 2005).

There was no correlation between biological data and any of the environmental factors. Despite the high level of correlation and significance between biomass and density ($R^2 = 0.75$****), neither of the factors were fully redundant, and the two were consequently analysed in parallel.

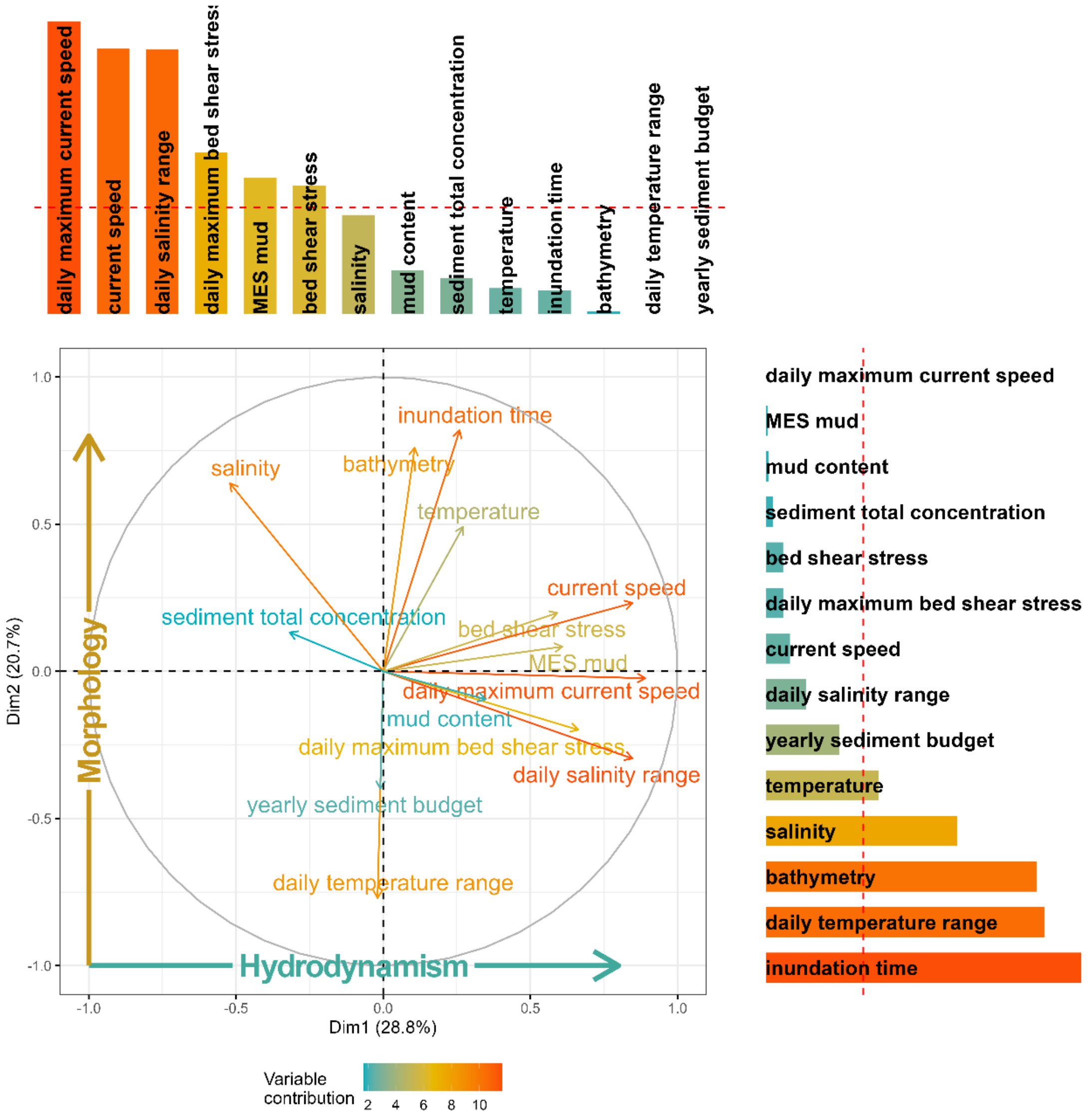

Figure 2: PCA variable correlation plot with the abiotic factors' contributions in bar plots for each axis. The red dotted line represents the mean contribution for all factors.

Table 2 PCA scores for abiotic factors

Variable	**Cos2**			**Contrib**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
inundation time	0.07	0.67	0.00	1.67	23.10	0.13
current speed	0.72	0.05	0.01	17.82	1.86	0.46
daily maximum current speed	0.79	0.00	0.01	19.65	0.02	0.42
salinity	0.27	0.41	0.03	6.71	14.04	1.23
daily salinity range	0.72	0.09	0.00	17.78	3.02	0.13
temperature	0.07	0.24	0.02	1.83	8.31	1.00
daily temperature range	0.00	0.59	0.01	0.01	20.44	0.52
MES mud	0.37	0.01	0.13	9.18	0.24	5.68
bathymetry	0.01	0.58	0.13	0.28	19.88	5.66

yearly sediment budget	0.00	0.16	0.01	0.00	5.47	0.38
bed shear stress	0.35	0.04	0.40	8.68	1.35	17.99
daily maximum bed shear stress	0.44	0.04	0.16	10.88	1.36	7.25
sediment total concentration	0.10	0.02	0.67	2.51	0.60	30.19
mud content	0.12	0.01	0.64	3.00	0.31	28.96

3.3 Description of the Hydro-Morpho-Sedimentary data

The selected predictors were observed during the same period and in the same area as the biological data (Supp. Data 3.3). Generally speaking, all the factors differed significantly in area and period:

- Daily maximum current speed [$m.s^{-1}$]: the most dynamic area was the channel, with a mean of 1.05 +/- 0.21. The northern upstream and median mudflats were subject to temporal changes in the distribution of the current in the last period, which had an impact on their global mean (upstream 0.43 +/- 0.34; median 0.63 +/- 0.3). The south mudflat had same hydrological conditions than offshore, in between north upstream and median mudflat.
- Inundation time [%]: The upstream mudflat, corresponding to upper intertidal areas, had higher tidal locations than the median mudflat, and shows a decrease in the last period. The south mudflat had higher inundation time than the north downstream mudflat, the latter being as subtidal than offshore and channel.
- Daily salinity range: This factor varied considerably in space and over time. Offshore and south mudflat, salinity varied little during the day. Strongly influenced by the river, salinity in the channel vary of 15-20 during the day, but with a reduction as time went by. The highly dynamic variations in salinity in the three north mudflats decreased after 2005.
- Temperature [°C]: A significant global increase in temperature was observed in all areas over time. The north median mudflat had the highest range, due to its intertidal location.
- Mud content [%]: The north upstream mudflat and channel areas were composed with sandy mud sediment (north upstream mudflat 42 +/- 30; channel 43 +/- 25) with an increase of mud content for the channel over time. The others are more muddy sands (21 +/- 1), with a decrease of mud content over time. Mud distribution was heterogeneous in all the areas, especially the north upstream mudflat.
- Daily maximum bed shear stress [$N.m^{-2}$]: as reflected in the current speed, the channel had the highest BSS (3.02 +/- 1.35), while the BSS in the other areas was similar (1.53 +/- 0.65) and progressively increasing. In the north upstream mudflat, the BSS drop down in the last period under 1.
- Bathymetry [m]: The depth of the channel and offshore were similar, with a mean range of 6.94-7.95. The north downstream mudflat and the south mudflat were the next deepest areas (4.16 +/- 0.95), the median mudflat was 1.77 +/- 3.3, and north upstream mudflat was the

shallowest, -1.59 +/- 2.63 (negative bathymetry being above the mean height of sea water) with again a drop at the last period.

3.4 Methodology assessment

All three calculation response models were used to build SDMs for each abiotic factor set at the different quantiles chosen. A general comparison of ΔAICc scores was undertaken for all the SDMs computed (Figure 3). The ΔAICc scores based on density were significantly higher than those based on biomass, and the choice of the quantile had a strong impact on the score. For instance, the best scores were obtained for the biomass SDMs with the 0.5 quantile, which would not help describe the optimum ecological niche. On average, the BSpline model ΔAICc were lower than the others (RQ2bsp = 2621 +/- 1643, RQ2nli = 2717 +/- 1713, RQ2int = 2739 +/- 1697). With the same biological response and quantile (biomass and tau=0.95), the variations between SDM ΔAICcs were quite low with respect to total variability (RQ2bsp = 1480 +/- 58, RQ2nli = 1529 +/- 49, RQ2int = 1575 +/- 39).

The predicted/observed plots (Figure 4 shows an example from set A), completed the observations of ΔAICc, i.e. RQ2bsp > RQ2nli > RQ2int (the regression lines of each quantile were closer to the 1:1 line). However, RQ2nli performed better than RQ2bsp at the 95th centile, which was defined as the optimum quantile, i.e. the highest quantile that did not affect model quality, and was hence used for all subsequent analyses.

Based on the range of both predictors under each set, the quantile responses of SDMs were calculated and illustrated by a surface plot (Figure 5 shows an example from set A, and interactive 3D plots are provided in Supp. Data 3.4). Although the performance indicators were good, graphically, the RQ2bsp model showed overfitting which prevented both modelling and prediction. This model was thus not used for any more analysis.

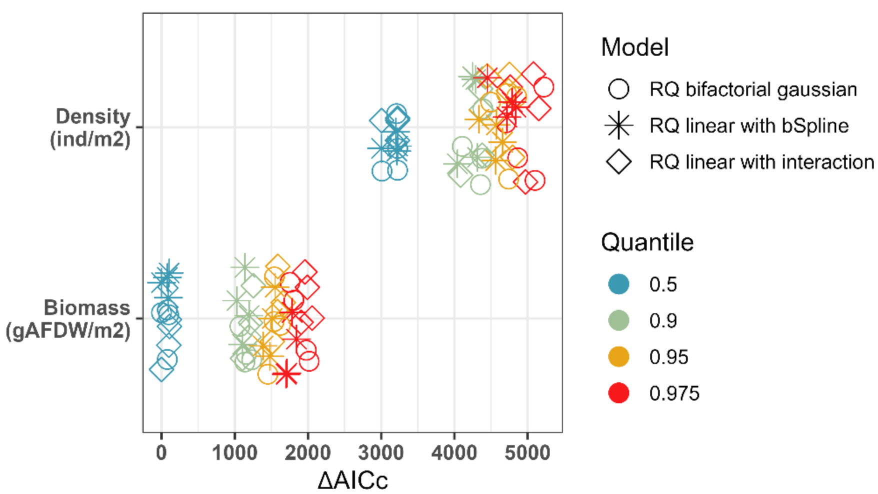

Figure 3: ΔAICc comparison for all SDMs computed, according to the quantile, the type of model and the response.

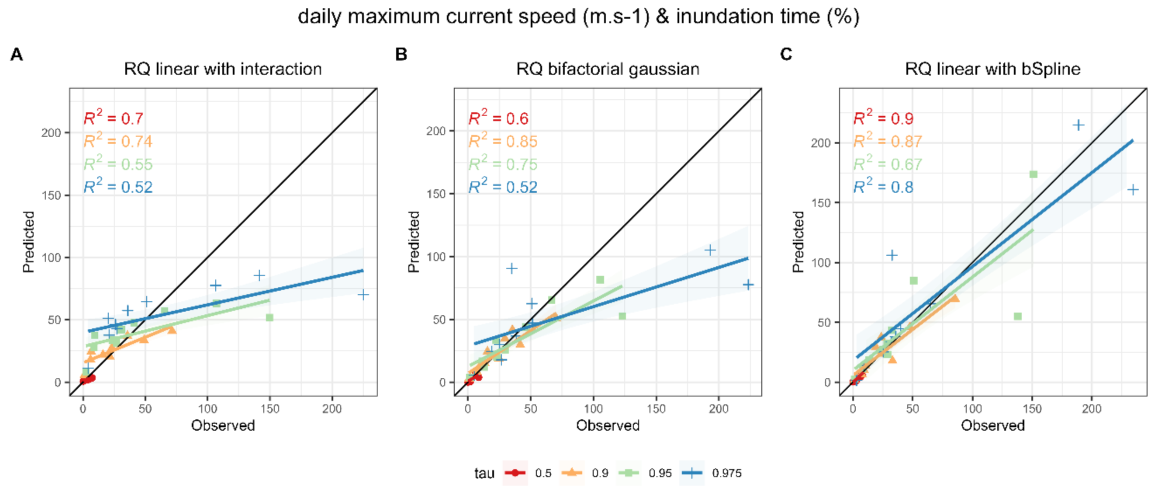

Figure 4: Example of modelled vs observed data plotted for each model based on biomass versus Daily maximum current speed [m.s^{-1}] and inundation time [%]. The black line represents the 1:1 ratio, quantiles 0,5 in red, 0.9 in orange, 0.95 in green and 0.975 in blue.

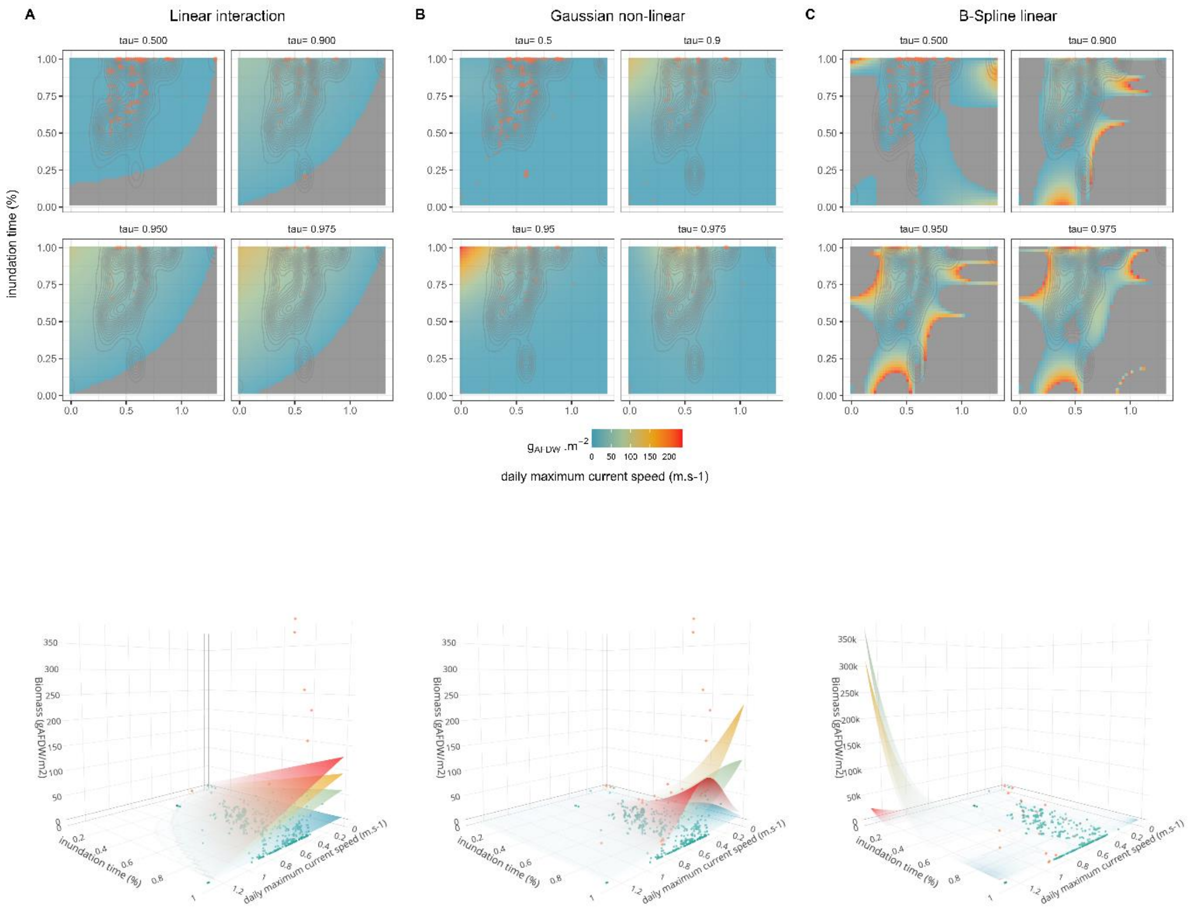

Figure 5: Examples of SDM surface plots under set A: linear with interaction (A), Gaussian non-linear (B) and Cubic B-Spline linear (C). The upper panels show for each of the four quantiles: the biological data observed represented by a contour plot, the model response in colour gradient surface and the observed data over the model are represented by red stars; the lower panel shows the 3D plots with all processed quantiles superposed.

3.5 Optimal ecological niche

3.5.1 Comparison of linear and nonlinear Quantile Regression

The four sets of models with 2 crossed abiotic factors (A, B, C and D, see 3.2 for details) were treated with one of the two selected models: either linear with interaction, or non-linear with a bifactorial Gaussian equation, with biomass as biological response (Figure 6, and SDM based on density, predicted/observed plot and RQ2nli SDMs in 3D graph are available in Supp. Data 3.5.1).

A. Daily maximum current speed [$m.s^{-1}$] & inundation time [%]: RQ2int optimum was 94.82 gAFDW/m² at 0 $m.s^{-1}$ and 100 %; RQ2nli optimum was 233 gAFDW/m² at 0 $m.s^{-1}$ and 100 %. The predicted/observed plot shows that RQ2nli performed better than RQ2int. The niche that was described was a lower intertidal zone with low dynamics, a combination that is rarely found in the HMS model.

B. Daily salinity range & temperature [°C]: RQ2int optimum was 68.96 gAFDW/m² at 0.2 and 13.01°C; RQ2nli optimum was 91.35 gAFDW/m² at 0.2 and 12.35°C. The observations fitted well with the optimum, and the performances of the two models were similar. The ecological niche corresponding to these models was the mouth of the estuary under temperate conditions.

C. Daily salinity range & bathymetry [m]: RQ2int optimum was 172.64 gAFDW/m² at 0.2 and 13.95 m; RQ2nli optimum was 147.6 gAFDW/m² at 0.7 and 5.14 m. The observed data were close to the Gaussian optimum, but not to the linear one, the plot predicted/observed by the non-linear model was better. With the HMS model, only a few parts of the estuary were less than 5 m deep, thereby excluding the linear model optimum. With the Gaussian model, the optimum niche was the end of the mouth of the moderately low intertidal estuary.

D. Daily maximum bed shear stress [Pa] & mud content [%]: RQ2int optimum was 104.58 gAFDW/m² at 100 % and 0 Pa; RQ2nli optimum was 106.94 gAFDW/m² at 35 % and 1.33 Pa. The non-linear model optimum was well represented by the observations, in contrast to the linear, even though the plots predicted/observed by both were good. The linear model was not in agreement with the knowledge provided by the biological model. The Gaussian model described a niche of muddy sand in a moderately active hydrodynamic area, likely undergoing erosion.

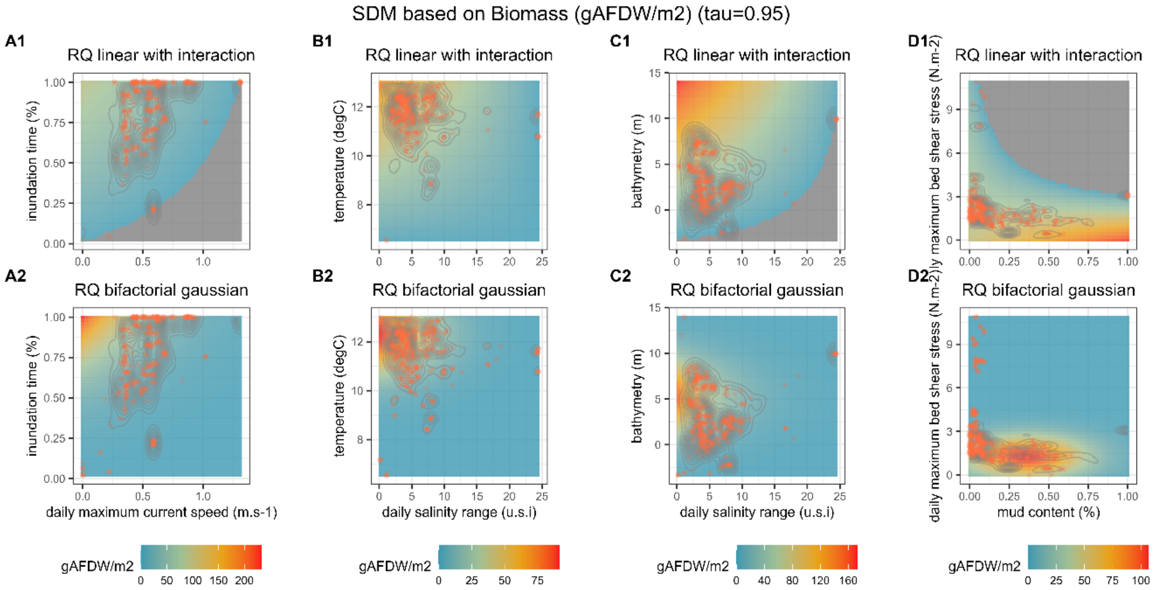

Figure 6: Sets of quantile regression models with 2 crossed abiotic factors (A,B,C and D see 3.2) computed with linear model (top row, numbered 1) and non-linear with the Gaussian equation (bottom row, numbered 2), the observed biological data under the model surface are represented by an isometric curve, the data over the model are represented by red stars. Each pair has its own range of biomass to ensure visibility.

3.5.2 Non-linear quantile regression with bifactorial Gaussian equation models

Overall, the non-linear model performed better than the linear model, and the density-based models were generally less relevant than models based on biomass (Figure 3). Thus, the quantile regression with bifactorial gaussian (RQ2nli) for biomass was the only model geographically applied and analysed, as the normalized suitability index. Each SDM for the RQ2nli model was applied on the HMS model web over the estuary, for each period (Figure 7, density in Supp. Data 3.5.2.1). The suitability index is given per period and area (Figure 8, density in Supp. Data 3.5.2.2, and suitability index compared to the two abiotic factor plot in Supp. Data 3.5.2.3), in detail:

A. Daily maximum current speed [$m.s^{-1}$] & inundation time [%]: The maps (Figure 7) showed that the channel and north mudflats were the least favourable areas, the south mudflats and offshore were more appropriate, but few locations were really optimum. The suitability index (Figure 8), which ranged from 0.1 to 0.3 and was generally stable, confirmed that the most suitable area was offshore, followed by south mudflat. The suitability of the north median and upstream mudflats improved after 2005, when they became better than the channel.

B. Daily salinity range & temperature [°C]: The salinity part of the model had a noticeable effect on the result of the model (Figure 7), with a clear reduction in biomass in the river and its ETM area. The closer the estuary entrance to the sea, the higher the model, the offshore area having a clear advantage that increased from 2005 on. The suitability index (Figure 8) ranged from 0 to 0.7. The three north mudflats underwent a significant increase during the first three periods. Offshore and south mudflats were similar and the most suitable, joined by north downstream mudflat at the last 3 periods, the channel being the least suitable area.

C. Daily salinity range & bathymetry [m]: The optima for this model were clearly located on the south mudflat (Figure 7), results linked to the bathymetry. Offshore, a spot was high in the period 1996-1999 caused by dumping material dredged from the channel that was subsequently progressively smoothed. Suitability index was less than 0.5, the south mudflat being the best (Figure 8). Apart from the north median and downstream mudflats which increased over the first three periods, the indexes for each area remained steady.

D. Daily maximum bed shear stress [Pa] & mud content [%]: This model result was very patchy at the scale of the estuary due to the equally patchy distribution of mud (Figure 7). This identified a channel with high biomass potential, which did not agree with expert knowledge. There was also an area with high biomass around the borders of the ETM area offshore which decreased over time, also due to the reduced mud content. Suitability ranged from 0.25 to 0.75 (Figure 8), with a complex pattern. The suitability of the channel, offshore, south mudflat and north downstream mudflat decreased after 2005, while the suitability of north u!pstream and median mudflats improved.

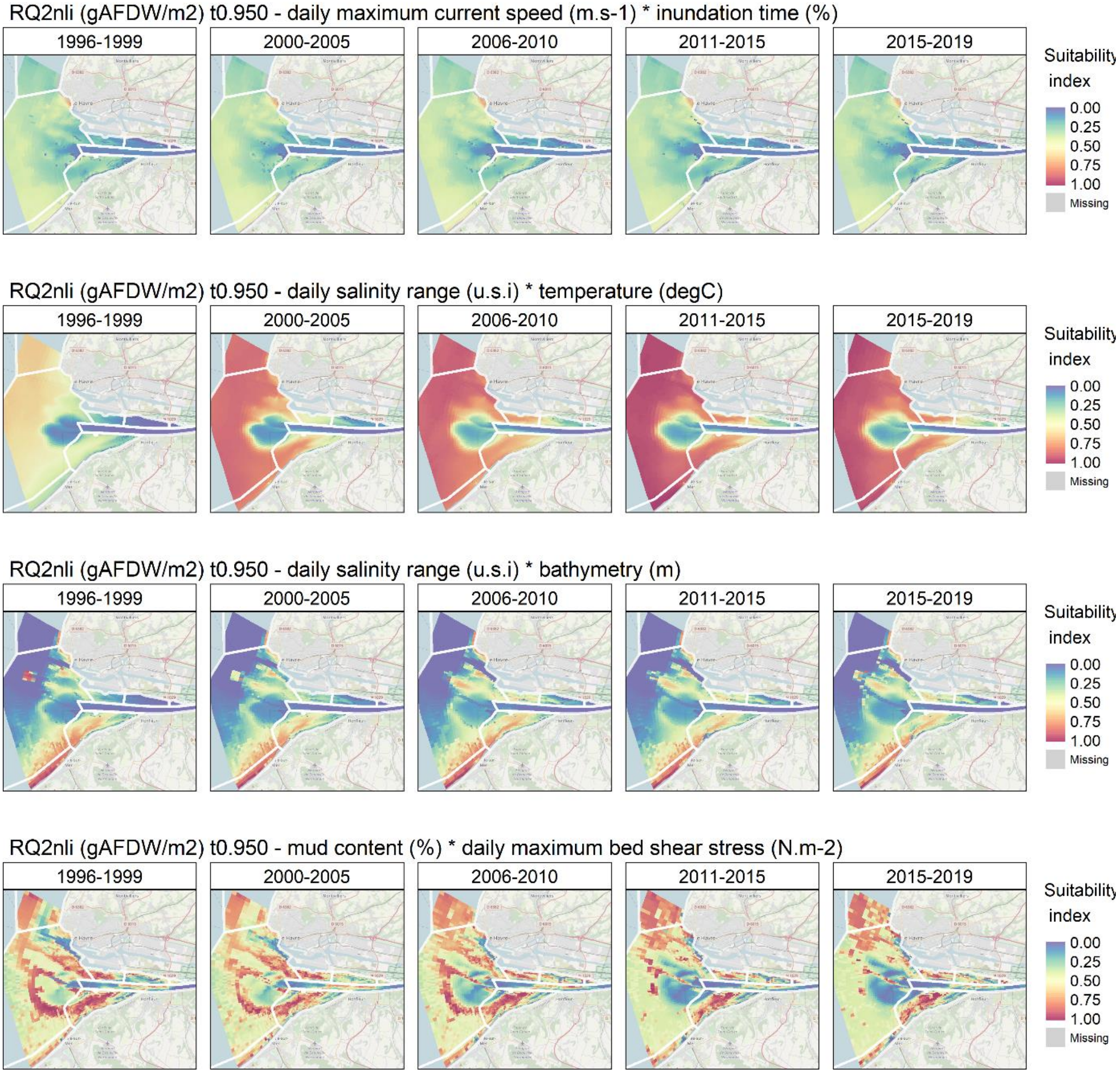

Figure 7: SDM models suitability index applied on the Seine estuary over the five periods.

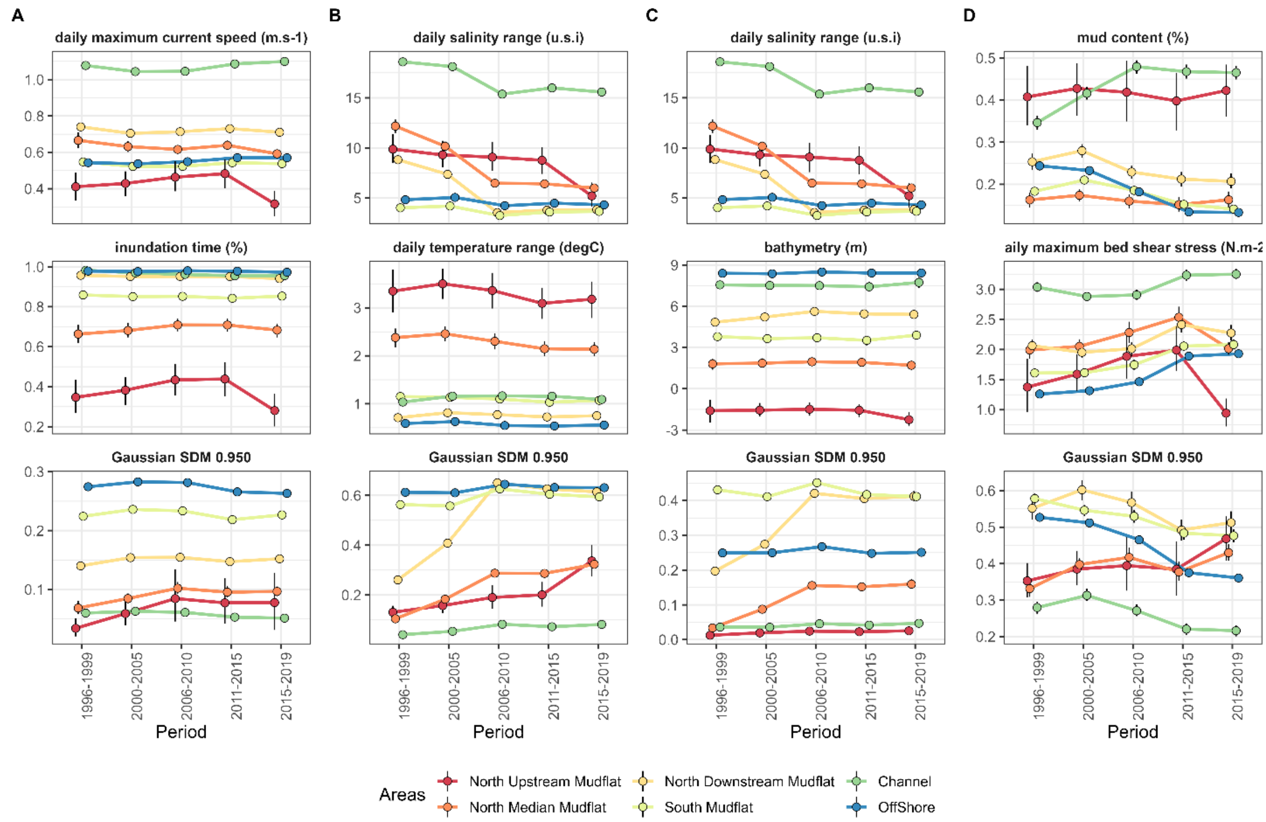

Figure 8: Abiotic factors and resulting SDM suitability index per period and per area for all SDM models with a 95% confidence interval.

4 Discussion

4.1 Assessment of the methodology

The quality of a SDM depends first and foremost on the reliability of the input data. The biological data used in this study comes from community monitoring programmes with a continuity of practices, and even of operators, which makes it possible to process data together over such a long period of time. Physical gradients condition complex interactions with fauna in estuaries (Chapman et al., 2010; Herman et al., 2001). However, community self-organisation also takes place at several overlapping spatial scales, strongly expressed by tidal constraints, where micro-scale organisations are able to create micro-climates (“shelters”) that can accommodate very high densities of fauna (Ettema and Wardle, 2002; Le Hir and Hily, 2005; Thrush et al., 2005; Underwood and Chapman, 1996). The abiotic field data, synchronous with the biological data, are more susceptible to highlight very small atypical habitats than macro-spatial trends. The use of a hydro-morpho-sedimentary model therefore makes it possible to better describe the overall “smoothed” environment. However, even if hydrological measurements and models are becoming increasingly reliable, modelling of the seabed and sediment transport still needs to be improved (Grasso et al., 2018). The complexity of an intertidal environment with its locally very different micro-habitats is difficult to portray on the scale of a model with a cell size of, at best, 100 m.

In order to align the biological data with the abiotic data, the latter were summarised at their annual median. With the exception of temperature, and to a lesser extent the daily maximum bed shear stress, the seasonal medians (winter from October to March and summer from April to September) do not differ significantly from the annual average. Nevertheless, the history of extreme events such as heat waves or storms is smoothed out, which is an obvious limitation of the study, as a punctual extreme event can lead to drastic changes in community succession initiated by a long-term change in physical conditions (Baltar et al., 2019).

SDMs can be constructed using an unlimited set of abiotic variables to define an ecological niche. However, an n-dimensional space is difficult to analyse from an ecological point of view as would be recommended (Austin, 2002). On the contrary, a single SDM predictor is possible, but it represents a risk of oversimplification that would result in an unreliable model. The choice of using two predictors, selected via a PCA analysis, makes it possible to further refine the description of an environment, and visualize the niche to confront it to ecological knowledge and intrinsic ecophysiological processes. In addition, we chose to present four SDMs, because it seemed reasonable to show different combinations of selected factors, rather than describing only one « supposed » best solution. Our sets have been designed to assess the impacts of different climate change effects on an estuary, while ensuring that the models can also be applied to other estuarine environments.

The quantile regression used in this study is interesting in that the biological response can be better modelled by two abiotic factors, even if there are other limiting factors. The abiotic data from HMS models can be used to describe complex patterns between the main physical factors, but at the very least they do not reflect the chemical variations (possible contamination) or biological interactions (competitive pressure, for example) involved in determining the dynamics of a population. Quantile regression at a high quantile level therefore makes it possible to limit the attenuating effects of factors not taken into account on the biological response.

There are experimental studies on the biological response to ranges of variation in temperature, salinity or even pH, which can provide a better understanding of the mechanistic basis of metabolisms on organism performance (Hale et al., 2011; Łapucki and Normant, 2008; Lemasson et al., 2017; Madeira et al., 2021; Medeiros et al., 2020; Ong et al., 2017; Peteiro et al., 2018). However, this type of approach cannot be applied to incorporate the effects of other physical factors. Exploratory methods based on long series of observations, such as those proposed here, remain one good method for integrating all the processes responsible for changes in habitability for populations such as cockles, without any preconceived ideas. It is known that physical stresses play a very significant role in the population dynamics of this species. Our study may enable us to make better progress in understanding the possible evolution of species on a multifactorial basis, before going further and validating new hypotheses through comparisons with other ecosystems or new experimental work in macrocosms, for example, enabling us to better identify the effects of all the factors.

This study compared a linear quantile regression to a non-linear quantile regression based on a bell-shaped curve and a B-Spline model. Considering only the AIC and the predicted/observed graphs, the linear model with B-Spline of the 3rd degree can appear efficient. However, even if the three calculation modes did provide a solution, the Gaussian model was the only adequate on an ecological point of view, that could truly rely upon specific traits. The choice of the observation quantile is a subject of discussion, as the SDMs produced very different results from one quantile to another. In this study, we chose to limit the number of quantiles to enable clear visualization of the models, but it is also possible to push the analysis to the point of looking for the highest quantile that still performs well. Yet, the aim of this study was to define the most favourable HMS conditions for the development of a species, not necessarily the niche representing the most exceptional circumstances. In fact, the very high quantiles will correspond to the niche that accounts for the biological observations resulting from the patchiness distribution of species.

4.2 Optimal ecological niches for cockles

When we compared the four sets of crossed factors (A: daily maximum current speed & inundation time, B: daily salinity range & temperature, C: daily salinity range & bathymetry, D: daily maximum bed shear stress & mud content), the quantile regression adjusted models revealed differences between them linked to the choice of predictors that led to different levels of expected biomass. Therefore, as the modelled biomass represent a carrying capacity that are difficult to observe, it was decided to compare the standardised results for each SDM.

The combination daily maximum current speed & inundation time (A) was based on the hydrodynamics generated by the meeting of the two masses of fresh and marine water under the effect of the tides and the fluvial regime (PCA1) and the morphology of the estuary, which generates shallow and intertidal areas (PCA2). Under these conditions, salinity increases with water depth, as it represents the upstream-downstream gradient of the estuary, and the greater the hydrodynamic conditions, the greater the mixing between fresh and marine waters. On the other hand, shallow waters follow day-to-day temperature variations more dynamically. The optimum of this model therefore represents a low intertidal marine niche, without intense variation in salinity and temperature. For the daily maximum current speed, this model shows an interesting variation in the niche between the 95th and 97.5th quantiles (Figure 5): the optimum of the 97.5th percentile (0.5 $m.s^{-1}$) is better represented by the observed data than the 95th, while the quantile plot shows a better performance of the 95th. 97.5th percentile shows that the cockle would have interest of having some hydrodynamics in their habitat.

Using inundation time rather than bathymetry as an abiotic descriptor was a better way to reflect the type of tidal of the estuary, in this case macro-tidal. The tide affects the feeding periods of the benthic fauna and the periods when they are accessible to predators, but also the daily hydrological conditions, as shown in set A. For their SDM, Cozzoli et al. used the same set of parameters with a higher centile, 97.5th, applied to a data set located in the Oosterschelde estuary, and obtained different results (Cozzoli et al., 2014). They observed that the optimum was found in a medium intertidal zone with a maximum current of 0.5 $m.s^{-1}$. It should be noted that the current range was wider than the range we obtained for the SDMs in this study.

The model using daily salinity range & temperature (B) is based on the same aspects of the estuary, only using the physico-chemical aspects of the water. The optimum niche for this model is low variations of salinity, hence the mouth of the estuary since the model is not calculated in its fluvial part. The optimum temperature is temperate (12.35°C) meaning that at upper temperature, the suitability decreases. This optimum corresponds to a little warmer than the global temperature found in the estuary, without the seasonal variability (12.15 ± 4.75°C), meaning that the cockle population is acclimated to the normal conditions found in their habitat. The optimum niche based on daily salinity range & bathymetry (C) is the same as the previous model regarding the salinity parameter, and the optimum bathymetry (5.14 m) corresponds to the low intertidal areas, almost subtidal, as shown in SDM A. This model is therefore aligned with SDM A describing the low intertidal mouth of estuary.

The model based on daily maximum bed shear stress & mud content (D) represents the hydrodynamics of the estuary (PC1) like the other 3 models, but adding another piece of information with the sediment composition of the estuary bed (PC3). The optimal daily maximum bed shear stress, corresponding to daily maximum current lower to 1 $m.s^{-1}$, is likely to generate erosion (1.33 Pa), but on the contrary to the model A, the absence of hydrodynamics is not the optimum, as would suggest the 97.5th quantile for model A. From a sedimentary point of view, the niche describes a muddy sand, which corresponds to what we know about the species.

Overall, when considering all bifactorial Gaussian quantile regression models, the best conditions for cockles appear to be in lower intertidal marine areas, with temperate and low dynamic waters, settled in muddy sand sediment. This description is in agreement with habitat EUNIS 2008 A2.242: *Cerastoderma edule* and polychaetes in littoral muddy sand (Tillin and Tyler-Walters, 2016; Tyler-Walters, 2007). Observations by Boyden and Russell in cockle habitats were similar, although these authors concluded that tidal flow was more determinant than salinity, the latter being an indirect indicator of the former in brackish waters, and that cockles were unable to settle in still water (Boyden and Russell, 1972). SDM A was more tolerant to still water at the 95th centile, but in agreement at the 97.5th centile.

4.3 A tool for ecosystem management

The SDM is a useful tool for environmental management, able to highlight any spatio-temporal differences in a given territory and makes it possible to monitor changes in physical parameters that are more accessible than data on species communities. In the present study, we chose to display the main results of SDM in the form of suitability index, based on simple normalization, to characterise the differences between two areas and between two periods. By making the SDM dimensionless, the index prevents interpretation of the result as the real amount of biomass. Still, as SDMs are linked to HMS variables, the suitability index is a good indicator of potential levers to cope with changes in suitability, particularly due to human activities, as well as with the effects of the global climate change.

When considering spatial application of the niches, an area under high human influence like the Seine estuary has HMS conditions that can be considered anomalies in the functioning of an estuary. The Seine channel is a major shipping route for the French economy and is therefore regularly dredged, and the sediment that is removed is dumped offshore. This artificial sediment transport not only modifies the bathymetry, but also the hydrological dynamics. As a result, certain areas of the estuary were applied but not included in the analysis of the results of the niche application: the Côte Fleurie and Octeville, the port and the beach of Le Havre are areas heavily disturbed by human activities. In addition, Cap Hève, south of the Octeville area, is an area with a bedrock substrate in which cockles cannot be present. The spatial application of the model must therefore be limited to areas where human impact remains reasonable. For this reason, the analysis of the suitability index focuses on the mudflats, with the channel and the offshore area as points of comparison.

As expected, all the suitability indexes show low values for the channel. North upstream and median mudflats are generally of the same range of suitability, quite low but slightly improving with time. North upstream mudflat shows a high range of variability, due to different conditions in the area. North downstream mudflat has an improvement of suitability, after 2005, to end at the same level than the south mudflat, except for SDM A, where it remains lower. The more suitable area was the south mudflat for all SDM, often at the same level as the offshore (expect for SDM C). The gradient from upstream to downstream is quite visible on all SDMs.

If we compare the temporal evolution of the index for the different zones with the evolution of the abiotic factors, we can see that the evolution of the daily salinity range is the parameter that has the greatest impact on the intertidal zones. For the northern upstream and median mudflats, the variation in salinity decreased after 2005, i.e. after the Port 2000 project, which increased the channelling of the estuary and therefore reduced the communication between the river and the tidal flats along its banks. In addition, the global temperature shows a significant increase over the years, especially in intertidal areas, which led to more suitability in SDM B. This model is the only taking into account the direct effect of temperature increases due to climate change, that is already visible in the period of data available. This model is the most sensitive to heat waves and presents a risk if extrapolated outside the model's definition range, as it does not take into account the acclimatisation of species in the niche, or at least the rate of acclimatisation in relation to the rate of warming of the waters of the estuary.

Although SDMs define optimum environments, they do not account for bioturbation or food-web processes, for example. Cockles are known eco-engineers which can modify their environment, especially sediment content (Donadi et al., 2014, 2013). They alter their habitat to obtain better conditions (Li et al., 2017), and interact strongly with the microphytobenthos, creating biofilms that alter sediment erosion properties (Eriksson et al., 2017; Ubertini et al., 2012). Those effects were assumed to be included in the variability of the response in all SDMs, but the processes themselves are inevitably hidden. Many of the processes involving fauna, flora and habitats have feedback loop effects, especially bioturbation, which have not yet been incorporated in HMS models, and the models thus fail to truly represent the mechanisms behind the species distribution. Even if self-organisation processes related to ecosystem engineering are totally masked by the SDM approach as direct factors, they must interfere and the best optimal habitat is in fact the one where self-organisation and other positive feedbacks [biogeochemical regulation by bioturbation processes and positive feedbacks with microphytobenthos production (Cade et al., 2005)]. This hypothesis could by tested experimentally to better refine the definition of optimal habitats.

A further limitation of this study is the use of a single species, *Cerastoderma edule*, but our method can be used for other abundant species present in the estuary, particularly species that are known to share the same habitats, such as *Macoma balthica*, *Scrobicularia plana*, *Hediste diversicolor*, *Corophium volutator* and *Peringia ulvae* (EUNIS habitat A2.24 : Polychaete/bivalve-dominated muddy sand shores (A2.241/MA5251, A2.242/MA5252, A2.243/MA5253) and A2.31 : Polychaete/bivalve-dominated mid estuarine mud shores (A2.312/MA6224, A2.313/MA6225) (European Environment Agency, 2023)). To go still further, it would be advantageous to develop a community scale indicator, based on the life traits, functional traits or ecosystem services the macrofauna can provide, as one species could progressively be replaced by another species that is equivalent from some points of view. Such upscaling would be important before applying the SDM to projections on a future representing the local effects of global climate change.

5 Conclusion

The development of accessible mathematical and statistical tools has considerably broadened the methodologies to build SDMs, and have been applied to different environments in dissimilar ways. Due to their complex structure and strong gradients, estuarine environments can benefit from the extraction of physical descriptors from models of water and sediment transports and the quantile regression approach. This tool helps define the areas that are suitable for targeted species based on a long time series data. However, the choice of environmental factors plays a decisive role in the result, and several models should be combined to obtain an overview of how the target fauna interacts with its environment. In this study, a suitability index is proposed as an indicator of the habitability of areas, based on a representative species, the cockle, but the index could be developed, as a prospect, into a community-based index, in order to take better account of the ecosystem services that the benthic macrofauna provides to the estuary.

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Figure 1 Maps showing the habitats defined in the dataset of the study area. Dots represent the location of the biological samples.

Figure 2: PCA variable correlation plot with the abiotic factors' contributions in bar plots for each axis. The red dotted line represents the mean contribution for all factors.

Figure 3: ΔAICc comparison for all SDMs computed, according to the quantile, the type of model and the response.

Figure 4: Example of modelled vs observed data plotted for each model based on biomass versus Daily maximum current speed [$m.s^{-1}$] and inundation time [%]. The black line represents the 1:1 ratio, quantiles 0,5 in red, 0.9 in orange, 0.95 in green and 0.975 in blue.

Figure 5: Examples of SDM surface plots under set A: linear with interaction (A), Gaussian non-linear (B) and Cubic B-Spline linear (C). The upper panels show for each of the four quantiles: the biological data observed represented by a contour plot, the model response in colour gradient surface and the observed data over the model are represented by red stars; the lower panel shows the 3D plots with all processed quantiles superposed.

Figure 6: Sets of quantile regression models with 2 crossed abiotic factors (A,B,C and D see 3.2) computed with linear model (top row, numbered 1) and non-linear with the Gaussian equation (bottom row, numbered 2), the observed biological data under the model surface are represented by an isometric curve, the data over the model are represented by red stars. Each pair has its own range of biomass to ensure visibility.

Figure 7: SDM models suitability index applied on the Seine estuary over the five periods.

Figure 8: Abiotic factors and resulting SDM suitability index per period and per area for all SDM models with a 95% confidence interval.

Table list

Table 1 List of types of models tested

Table 2 PCA scores for abiotic factors