A novel quantile regression approach to define optimal ecological niche: a case study on habitat suitability of cockle populations (Cerastoderma edule)

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A NOVEL QUANTILE REGRESSION APPROACH TO DEFINE OPTIMAL ECOLOGICAL NICHE: A CASE STUDY ON HABITAT SUITABILITY OF COCKLE POPULATIONS (*CERASTODERMA EDULE*)

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Abstract

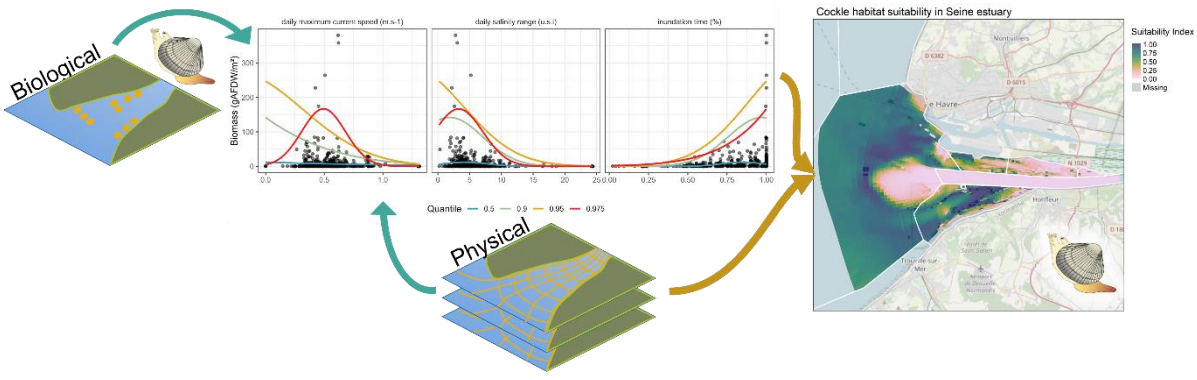
Correlative Species Distribution Models (SDMs) are powerful tools for understanding the spatial structure of ecological patterns and serve as a foundation for predicting the short-term effects of environmental changes on biological populations and for improving ecosystem management. However, due to complex and often non-linear interactions between biotic and abiotic factors, as well as irregular data distributions, SDMs are notoriously challenging to construct and validate, highlighting the need for continued research and methodological advancements in this active field of study. Quantile regression is a promising statistical technique to improve SDM as it can deal with data heteroskedasticity and provide a description of habitat suitability consistent with Liebig's Law of the Minimum. The aim of this study is to propose a tool for assessing habitat suitability of an estuary for a species, by defining its optimal ecological niche, which can be used for estuarine management, with a study case of *Cerastoderma edule* in the Seine estuary. The method involved applying quantile regression to a 20-year biological dataset coupled with a hydro-morpho-sedimentary model data set validated over a 25-year period, both at the scale of the estuary. To account for the complex distributional shapes, this study was carried out comparing three different types of equation (linear, Gaussian and B-spline). On the basis

of a preliminary multivariate analysis of the physical descriptors, two models were built representing hydrodynamic, morphodynamical and sedimentary features: daily maximum current speed, inundation time and daily salinity range or mud content as a third predictor. The Gaussian quantile regression produced the best description of the optimal niche, at the 97.5th centile and using the biomass. The optimal ecological niche for *C. edule* appeared to be lower intertidal marine areas, with low current speed, low salinity fluctuation and a sediment bed composed of muddy sand in the Seine estuary. The calculation of suitability index in this ecosystem was explored over a period of 25 years and analysed in isolated sectors to be applied in different scenarios related to global warming. The model using daily maximum current speed, inundation time and daily salinity range was also applied to data from the Scheldt basins, to test the reliability of the model, thus demonstrating that the model performs quite well, even though there were some differences of habitat suitability between these estuaries. This approach can allow direct comparisons of SDMs with one single Gaussian model and may offer new perspectives to investigate SDMs on a large scale.

Highlights

- Gaussian quantile regression at the 97.5th centile was the most performant model to define the optimal ecological niche of *C. edule* at the scale of the Seine estuary.
- Daily maximum current speed, inundation time and daily salinity range were the predictors the most adequate to build the optimal ecological niches.
- Optimal *Cerastoderma edule* conditions corresponded to low intertidal marine shores, moderate current speed, low salinity fluctuations in muddy sand sediment.
- The best model applied to the Scheldt basins shows some differences in the definition of optimal habitat compared with the Seine.

Graphical abstract



Keywords

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

Manuscript

1 Introduction

A species distribution model (SDM) is an approach that provides practical information on the spatial distribution of species based on ecological niche modelling (ENM) by investigating correlative interaction to predict the occurrence or the abundance of species as function of predictor variables. An ENM is defined in an n-dimensional environmental space that can be geographically projected as a SDM, providing managers and decision-makers with information about species distribution to help stakeholders to define conservation plans (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), the latter being based on eco-physiological laws. 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 (Melo-Merino et al., 2020; Robinson et al., 2011, 2017).

Correlative SDMs link the presence-absence or population quantitative information (abundance, biomass) of a targeted species with spatio-temporal habitat data, thereby quantifying the relation between environmental factors and species distribution (Elith and Leathwick, 2009; Franklin, 2010; Guisan and Thuiller, 2005). These methods generally use geo-localised biological data of a species and abiotic parameters measured by techniques such as remote measurements or modelling (Brown et al., 1996; Guisan and Zimmermann, 2000; Melo-Merino et al., 2020; Van Der Wal et al., 2008).

Correlative SDMs encompass a multiplicity of statistical techniques, which can be divided into two approaches: algorithmic modelling (AM) and data modelling (DM) (Warren and Seifert, 2011). AM methods, such as MaxEnt or random forest, involve a statistical comparison of abiotic and biological data, without defining the type of relationship, embracing the overall intrinsic complexity of the environment, with the aim of maximum prediction performance, but without describing the physiological processes involved. These methods have recently undergone considerable development, thanks to the increasingly easy access to the computer tools needed to implement them, they have been applied for instance on cockle populations (Matos et al., 2023; Singer et al., 2017). The DM approach, which is more historical, consists of defining *a priori* a type of relationship between abiotic factors and biological response, based on the state of the art of the species and its environment, in a principle of parsimony and simplification of the description of an environment. The aim is then to highlight the main physiological

processes explaining population dynamics, and to provide tools that can be applied in spatially and temporally diverse contexts.

In the context of a DM approach, various regressions techniques can be used, which are often based on Ordinary Least Squares (OLS), which defines the conditional mean function between the biological response and selected predictors (Koenker and Hallock, 2000). Whatever the number of factors used, there will always be unmeasured or unknown factors, which may have a limiting effect on the biological response, which then reflects the response to these unknown limiting factors. This is the statement of Liebig's law of minima: if other resources are not optimal for some observations, the measured response of the species will be lower than the maximum possible response to the recorded resource (Anderson, 2008; Cade and Noon, 2003). This generates heteroskedasticity in bivariate or multivariate data distributions, as the mean and variance of the species abundances along environmental gradients tend to be positively correlated, thereby violating one of the fundamental assumptions of OLS modelling. It follows that the construction of a OLS-based SDM cannot take into account all meteorological, hydrodynamic, morphological or sedimentary factors, such as 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) that may partly bias the biological response to a set of selected factor (Austin, 2007; Cade et al., 1999).

The use of quantile regression (QR) can counteract this limitation, by defining different quantiles of biological response depending on the abiotic factors chosen (Koenker and Hallock, 2000; Koenker and Machado, 1999). Studies have been conducted for more than 40 years to apply QR, and recent advances in computer tools have improved its use and facilitated its interpretation especially for ecological applications, such as SDM (Austin, 2007; Cade et al., 2005, 1999; Cade and Noon, 2003; Jiménez-Valverde et al., 2021). The variability of the biologic response to a fixed environmental condition could be considered to reflect the expression of other more or less limiting factors. By targeting the upper quantiles in a QR, it is possible to define the best maximum biological response to selected abiotic predictors, with any other factors, whether biological, environmental or mobility being considered as non-limiting (Schröder et al., 2005). In other words, while classical ENM focus on modelling the average response to the environment, QR ENM focus more on modelling extremes, thus providing a description of species abundance distribution consistent with the theoretical principle of Liebig's Law. The modelling of extremes, if based on a sufficiently rich dataset (over the long term, in various environmental conditions), has the potential to outline the boundaries of species niches, describing what we named Optimal Ecological niche (OEN), by removing particular conditions recorded (meteorological conditions, sanitary events, lifespans).

This type of OEN can be a key tool for estuarine and coastal management in the context of climate change and anthropogenic pressures (Crossland et al., 2005; Grassle, 2013). Indeed, understanding the links and interactions between abiotic and biotic components is necessary to preserve biodiversity and restore areas affected by environmental fluctuations and human activity, in order to conserve the benefits of their functional ecosystem services (Richards and Lavorel, 2023). Among a vast list of ecosystem services, an estuary is a shipping lane, a fishing ground and an area comprising diverse

natural habitats (Hughes et al., 2014). All these activities compete for space and have different needs and yet are linked to each other, so it is necessary to have decision support tools that improve their management and enable their future development (Degraer et al., 2008; He et al., 2015; Schickele et al., 2020). In particular, the vulnerability of estuarine sediments to the sea level increase and coastal squeeze has been identified for a long time with a strong negative impact on the trajectory of tidal flats (Healy et al., 2002; Murray et al., 2019). Many studies highlight the relevance of ecological gradients in estuaries (Brown et al., 1996; Guarini et al., 1998; Van Der Wal et al., 2010), where intertidal areas are undeniably subject to massive and frequent gradients, due to both actions of the tide and the river discharge, modifying the physico-chemical environment of water bodies. Physical gradients drive the set of interaction links with fauna in estuaries (Chapman et al., 2010, p. 20; Herman et al., 2001).

Within estuarine fauna, benthic macrofauna (or macrozoobenthos) is a key element in ecosystem functioning. Often primary consumers, they are a source of trophic support for the higher levels, in particular for fish and shorebirds (Saint-Béat et al., 2013). Their presence on or in the sediment contributes to sediment biogeochemical fluxes and morphological dynamics of their environment through a series of eco-engineering processes (Arlinghaus et al., 2021; Jones et al., 1994; Kristensen et al., 2012). 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 and stressful conditions (erosion, mud accumulation, anoxic episodes…). 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). It is therefore very relevant to focus on the response of macrozoobenthos not only to temperature or salinity changes, but also to physical dynamics occurring in an estuary (Shi et al., 2020; Van Der Wal et al., 2017) such as sea level rise, increases in wave and current intensity related to more frequent storms or also the risk of coastal squeeze.

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 temporal projection on a regional spatial scale and therefore to develop climate-focused forecasts and scenarios. On the basis of this available information, on both biological and abiotic components, it is then possible to model the

spatial distribution of the targeted species, in order to better define the fauna-environment interactions that shape the presence and the performances of the species in the estuary under consideration.

Investigating populations of *Cerastoderma edule*, the common cockle, as an example in the Seine estuary, the aim of this study is to assess the ENM following the principles of the DM approach, with the biological response (biomass and density) as a function of the hydro-morpho-sedimentary factors of the estuary extracted from a 3D model. With the aim of proposing an OEN transferable to other estuarine environments, we used quantile regression at higher quantiles, with either linear or non-linear curve responses (Gaussian and B-spline). While linear responses are the simplest, there's a danger of oversimplifying species-environment relationships as in nature there are often "shortages" or "surpluses". Furthermore, univariate linear relationship cannot account for the effect of subsidiary factors the responses to which are inversely correlated with the variable of interest. For instance, the preference of *C. edule* for the intermediate tidal flat can be intended as a combination between a positive response to submersion time (longer feeding time) and negative response to increased current velocity (dislocation). As a large number of subsidiary factors generally interact in shaping species distribution along single gradients, Gaussian responses are useful for modelling species with a clear environmental optimum, but still oversimplify the effect of interactions with co-varying subsidiary factors. Flexible shape responses (like B-splines) provide a more nuanced view, capturing asymmetry in species responses to environmental gradients, but less intuitive and more data-intensive. Building on the work done by (Cozzoli et al., 2017, 2014, 2013), we propose to take the use of QR a step further by 1) showing that using a Gaussian equation rather than a linear or B-spline equation is more appropriate to describe a typical biological response, 2) building two models based on three environmental variables to reflect the effects of hydrodynamic (including meteorological), morphological and sedimentary processes in an estuary. These models were applied and analysed geographically in the Seine estuary, in the form of suitability indices, as a tool for developing conservation and management plans. In addition, one of the models was applied to an independent dataset from the Scheldt estuary (Cozzoli et al., 2014) in order to discuss the transferability potential of an ENM for cockles at a more global scale.

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.

2.1 Study area

The Seine estuary in Normandy, north-west France, is defined as the last 170 km of the river leading to the marine ecosystem close to Le Havre, starting at Poses weir upstream and ending in the bay of Seine downstream. The Seine estuary is macrotidal (with a maximal tidal range of 8 m during spring tides at Honfleur), and is subject to fresh water discharge 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; Lesourd et al., 2003; 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 constitute areas of major interest including nutrient recycling, coastline protection, trophic networks, nesting sites for migratory birds and fish nurseries. The Seine estuary is marked by artificial 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 were built and sediment dredging was 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, hence provoking a "coastal squeeze". Some of these works were large-scale projects: the construction of the Pont de Normandie (1989-1995), which crosses the Seine estuary, and the "Port 2000" project (2000-2005) to expand the port of Le Havre, mainly to give large container ships access to new all-day loading berths.

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 to serve as a resting place 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 intertidal mudflats and subtidal areas (Morelle et al., 2020; Tecchio et al., 2016) (Figure 1).

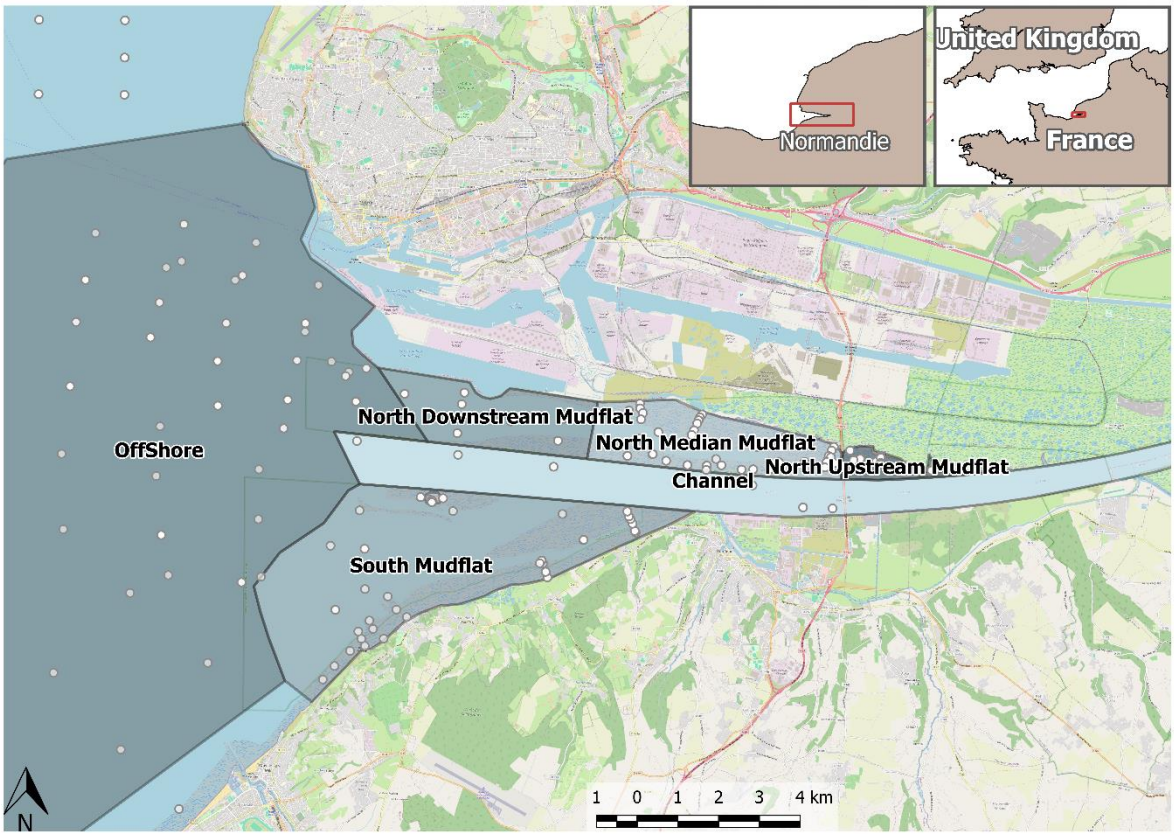


Figure 1 Maps showing the habitats defined in the dataset of the study area. Dots represent the location of the biological samples.

2.2 Biological model

The cockle *Cerastoderma edule* (Linnaeus, 1758) is a bivalve belonging to the family of Cardiidae that is widely distributed and exploited in waters off northern Europe 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 phytoplankton in the adult stage (Sauriau and Kang, 2000). It provides numerous ecosystem services (Carss et al., 2020), and is a bioturbator species actively studied for its effects on sediment morphology (Eriksson et al., 2017). 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). Assessment of habitat suitability and SDM in previous studies mainly report the relevance of submersion (Cozzoli et al., 2014; Matos et al., 2023; Singer et al., 2017), salinity (Matos et al., 2023), temperature (Singer et al., 2017) and current velocity (Cozzoli et al., 2014).

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 were harmonised and grouped in a single database which contains a total of 543 observations of *Cerastoderma edule*, and 86 sampling stations (with some variation in coordinates from year to year), with an average of 24 stations sampled in each campaign (depending of the project), mainly in September, October, and November. A series of 5-year periods was defined within the duration covered by the dataset, from 2000 to 2019 (the years before 2000 were discarded as they contained too few observations, n = 17): 2000-2005, including the construction of 'Port 2000' which caused major disruptions in the estuary; 2006-2010; 2011-2015; 2016-2019. These periods correspond to identified hydro-morphological sequences in the estuary.

2.3.2 Hydro-Morpho-Sedimentary data

The HMS model 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). This MUSTANG module takes into account spatial and temporal variations in sand and mud content in the multi-layered sediment bed, as well as consolidation processes, and also solves 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 HMS dataset was generated during the ARES project using the Mars3D model (Grasso et al., 2021, 2019). 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. Inundation rates were indirectly calculated from bathymetry and water height of the model. 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 retained variables retained were the total thickness of the sediment and the bed shear stress. (Grasso et al., 2018) validated the Seine Estuary model in terms of hydrodynamics, salinity, and SSC from tidal to annual time scales at different stations within the estuary, the sediment fluxes were considered more qualitative (Grasso et al., 2021).

In addition to these variables, processing was carried out to extract supplementary 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 reduced to a median calculated over the hydrological year. Biological data were associated with HMS variables corresponding to the model cell and the relevant hydrological year according to the sampling date.

These 14 abiotic factors were studied to select the most relevant factors and limit their number in order to avoid autocorrelations. A PCA (`FactoMineR::PCA` (Husson et al., 2024) and `factoextra` (Kassambara and Mundt, 2020) package for visualisation) was carried out on all the factors, allowing complementary parameters to be identified on the two main axes. In addition, a correlation matrix with

the biomass and density of *C. edule* ensure that there was no direct correlation between abiotic and biotic factors.

2.4 Model adjustments

2.4.1 Quantile regression

The mathematical theory of the quantile regression (QR) has been extensively expanded and described by Koenker over the past 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 since the first pioneering studies (Cade et al., 2005, 1999; Cade and Noon, 2003).

In practice, correlative ENM with QR can use any type of equation that links abiotic factors to a biological response, with any number of predictors to be used. Yet it was observed that the biological response to physical factors is often non-linear, and can be modelled by a gaussian distribution (Huisman et al., 1993; Van Der Wal et al., 2008). With this in mind, we have defined three different types of models in this study (Table 1) to describe the interplay of three abiotic factors to the biological response, by testing different functions (linear, B-spline and Gaussian). 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 et al., 2024). The three model types were computed with different quantiles τ = [0.5, 0.9, 0.95, 0.975].

The model was adjusted on the biological data with the associated HMS data to create ENMs, which were then applied to the HMS data set, focused on the estuary. The maximum of each quantile of the ENM was used to standardise the model response, in order to create a suitability index, ranging from 0 to 1. The results are displayed in maps with the mean of the model over each period, for each cell. A mean of the suitability index by area and period is calculated to visualise the global suitability over the whole estuary and the contribution of each factor.

Table 1 List of types of models tested

Type	Equation	Rationale
RQ linear with interaction	$y_\tau = \beta_{0\tau} + \beta_{1\tau}.x_1 + \beta_{2\tau}.x_2 + \beta_{3\tau}.x_3 + \beta_{4\tau}.x_1.x_2 + \beta_{5\tau}.x_2.x_3 + \beta_{6\tau}.x_1.x_3 + \beta_{7\tau}.x_1.x_2.x_3$ `quantreg::rq(x1*x2*x3)`	Comparison with the results of a previous study (Cozzoli et al., 2014)
RQ gaussian (non-linear)	$y_\tau = \mathrm{A}.e^{-\left[\frac{(x1-\mu1_\tau)^2}{2.\sigma1_\tau^2}+\frac{(x2-\mu2_\tau)^2}{2.\sigma2_\tau^2}+\frac{(x3-\mu3_\tau)^2}{2.\sigma3_\tau^2}\right]}$ `quantreg::nlrq(f(x1,x2,x3, initial.conditions))`	Providing μ and σ initiated by the mean and the standard deviation for each predictor (Huisman et al., 1993; Schröder et al., 2005).
RQ linear with B-Spline	`quantreg::rq(splines:: bs(x1,degree=3,knots= median(x1))+ bs(x2,degree=3,knots= median(x2))+ bs(x3,degree=3,knots= median(x3)))`	Avoid pre-determined shape of the equation and the use of a flexible 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. 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 the AIC, the relationship between predicted and observed values was plotted to establish a validation plot (Cozzoli et al., 2014). The whole dataset was sampled with random replacement. The predicted (model output) data were discretized in 10 homogeneous classes based on the predicted values and for each class, the correspondent sample quantile of the observed data was calculated. To assess the validity of the modelled quantiles, a linear correlation was drawn for each quantile between random-predicted and observed values.

3 Results

3.1 Description of the biological data set

The biological dataset for *C. edule* was split into four periods: 2000-2005 (n = 108), 2006-2010 (n = 155), 2011-2015 (n = 174), 2015-2019 (n = 106). The following treatment focussed on the mudflats inhabited by *C. edule* (south mudflat (n = 218), north median mudflat (n = 198), north downstream mudflat (n = 82), north upstream mudflat (n = 2). The differences in biomass and density are detailed according to the period and the surface area concerned in Supp. Data 3.1.

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

The selected predictors were observed during the same period and in the same area as the biological data (Supp. Data 3.2). Spatio-temporal variations were specific to each factor:

- Daily maximum current speed [$m.s^{-1}$]: the most dynamic area was the channel, with an average of 1.05 +/- 0.21 $m.s^{-1}$. The northern upstream and median mudflats were subject to temporal changes in the distribution of the current during the last period, which had an impact on their overall average (upstream 0.43 +/- 0.34 $m.s^{-1}$; median 0.63 +/- 0.3 $m.s^{-1}$). The southern mudflat presented the same hydrological conditions as offshore, at values between those of the northern upstream and median mudflats.

- Inundation time [Proportion of the tidal cycle between 0 and 1 without unit]: The northern upstream mudflat (0.4 +/- 0.36) corresponded to the upper intertidal zones and showed higher tidal locations than the median (0.7 +/- 0.35) and downstream mudflats (0.93 +/- 0.17). There was a decrease in inundation time during the latest period in the northern upstream mudflat. The southern mudflat (0.85 +/- 0.27) showed a shorter inundation duration than the northern downstream mudflat.

- Daily salinity range: This factor varied considerably over space and over time. On the offshore and southern mudflats, the salinity varied little during the day. Strongly influenced by the river, the channel salinity varied from 15 to 20 during the day, but with dampening over time. The very dynamic variations in salinity in the three northern mudflats decreased after 2005.

- Mud content [%]: The northern upstream mudflat and channel areas were composed of sandy mud sediment (north upstream mudflat 42 +/- 30 %; channel 43 +/- 25 %) with increasing mud content in the channel over time. The others are muddy sands (21 +/- 1%), with decreasing mud content over time. Mud distribution was heterogeneous in all areas, particularly in the northern upstream mudflat.

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 corresponded to the hydrodynamic forcing of the area with the contributions of the following variables: daily maximum current speed (19.6 %), average current speed (17.8 %), daily salinity range (17.8 %), daily maximum bottom shear stress (10.9 %), SPM (9.2 %), average bed shear stress (8.7 %).
- PC2 was related to the morphology of the estuary with the contributions of the following variables: average inundation time (23.1 %), daily temperature range (20.4 %), average bathymetry (19.9 %), average salinity (14 %), average temperature (8.3 %).
- PC3 was related to the sedimentary characteristics of the bed with the contributions of the following variables: average sediment total concentration (30.2 %), average mud content [<63 µm] (29 %), average bed shear stress (18 %), daily maximum bed shear stress (7.2 %).

The PCA results were used to select predictors to capture the most relevant and transferable variables. Considering those axes, two models were built with three abiotic factors:

A. Daily maximum current speed [$m.s^{-1}$] & daily salinity range & inundation time [%] – PC1-PC1-PC2: variables were the main contributors of the two first axes, but the third axis is not represented at all. We have made this selection because these 3 predictors can be easily retrieved at high frequency in other ecosystems or contexts. Those parameters 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 river floods, both processes in relation to climate change. The daily salinity range is a good indicator of the estuarine condition, and have shown a high impact on *C. edule* patterns (Matos et al. 2023). Moreover, this selection makes possible the direct comparison with a previous study (Cozzoli et al., 2014).

B. Daily maximum current speed [$m.s^{-1}$] & inundation time [%] & mud content [%] – PC1-PC2-PC3: These factors represented the main contributors of the three first axes of the PCA. Moreover, current speed and inundation time are easily measurable at high frequency (Goberville et al., 2010). They illustrate three aspects of climate change potentially able to alter spatial patterns of cockles: increase in storm-induced currents, global sea level rise and

general changes in sediment beds induced by erosion events that could be more frequent as a consequence of the global warming. Furthermore, the mud content could affect negatively *C. edule* habitability (Folmer et al., 2017).

There was no significant linear correlation between biological data and any of the environmental factors. Despite the high level of correlation and significance between biomass and density (R = 0.866****), these two variables were analysed in parallel.

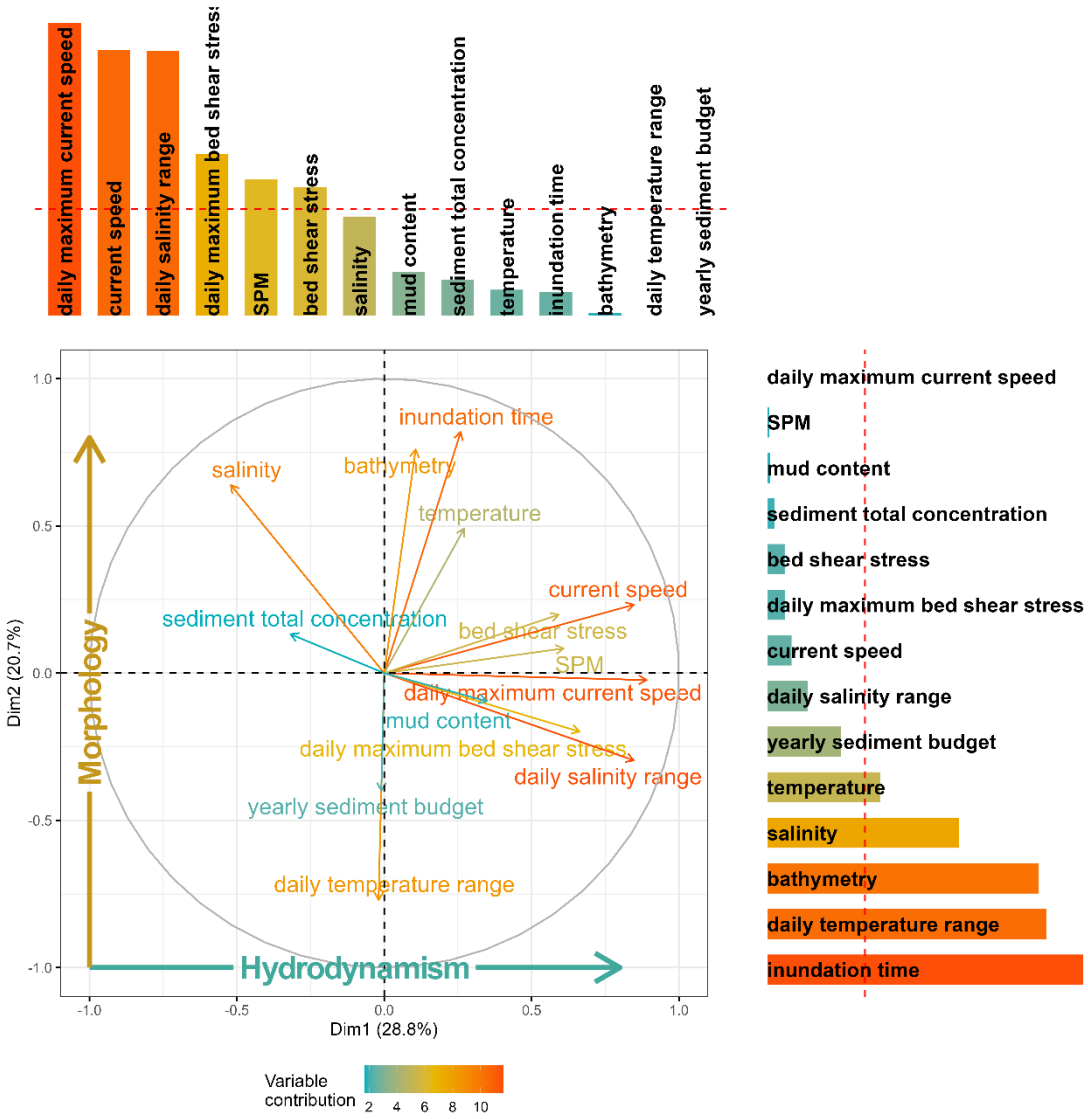


Figure 2: Principal Components Analysis (PCA) variable correlation plot with the abiotic factors' contributions in bar plots for each axis. The red dotted line represents the mean contribution for all factors.

*Table 2 Principal Components Analysis (PCA) scores for abiotic factors. Cos2, cosine squared of the variables, represents the quality of the representation of the variables on the PCA graph; Contribution represents the contributions (in percentage) of the variables to the principal components. The contribution of a variable to a given principal component: (Variable.cos2 * 100) / (total cos2 of the component).*

Variable	Cos2			Contribution		
	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
SPM	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 Model selection and validation

ENMs were computed using the three equations (linear, Gaussian and B-spline) for each combination of abiotic factors at four selected quantiles (τ=0.5, 0.9, 0.95 and 0.975). The best scores were obtained for the biomass models compared to the density models, regardless of quantile. On average, the AICc of the quantile regression with the Gaussian equation model were systematically lower than the others for biomass (Table 3).

The validation plots comparing observed and predicted values (Figure 3), completed the observations of AICc, i.e. Gaussian > B-Spline > linear (the regression lines of each quantile were closer to the 1:1 line). The Gaussian equation performs best at the 97.5th percentile, since this is the highest quantile calculated with the slope of the regression line between the predicted value and the observed value closest to the 1:1 diagonal. We have therefore chosen to retain the 97.5th percentile as the optimal quantile for subsequent analyses.

Table 3 AICc comparison for all models computed, according to the quantile, the type of equation and the response. In bold, the lower value of each model by response and quantile.

	Biomass (gAFDW/m²)				Density (ind/m²)			
	0.5	0.9	0.95	0.975	0.5	0.9	0.95	0.975
daily maximum current speed (m.s-1) & daily salinity range & inundation time (%)								
Quantile regression bSpline	3858.7	4933.4	5297.1	5668.9	6977.6	**8065.7**	**8403.0**	**8634.6**
Quantile regression Gaussian	**3835.0**	**4871.2**	**5240.9**	**5655.3**	**6969.1**	8102.2	8476.1	8783.3
Quantile regression linear	3869.9	4918.5	5292.3	5702.6	6985.0	8067.4	8404.4	8706.1
daily maximum current speed (m.s-1) & inundation time (%) & mud content (%)								
Quantile regression bSpline	3745.4	4790.6	5148.1	5496.5	6758.8	7794.7	**8126.5**	**8283.2**
Quantile regression Gaussian	**3733.7**	**4746.8**	**5071.5**	**5418.7**	**6745.2**	7819.8	8186.1	8533.3
Quantile regression linear	3757.0	4794.8	5162.0	5527.7	6767.1	**7815.0**	8142.6	8361.2

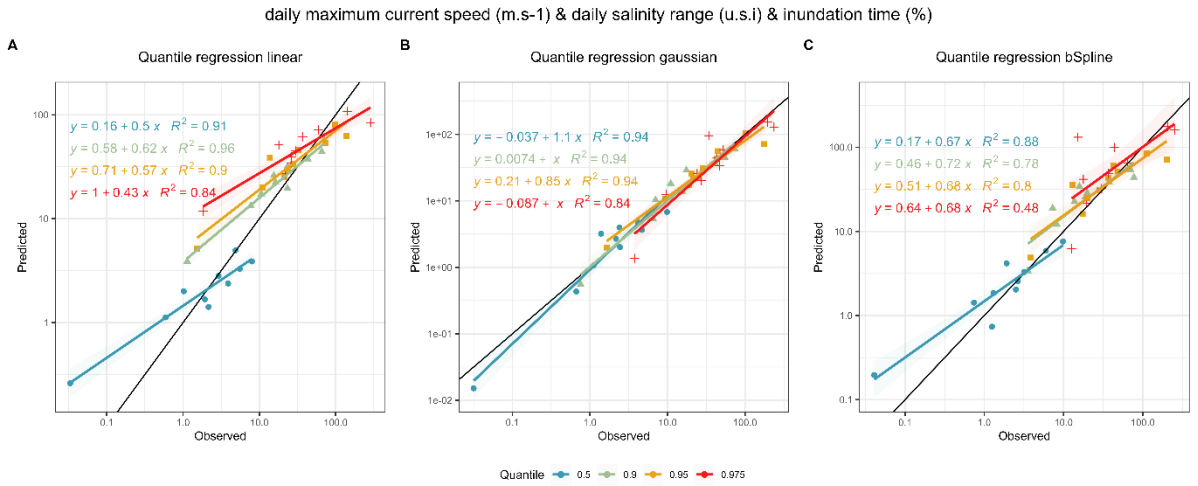


Figure 3: Example of modelled vs observed biomass data plotted for each model functions. The selected predictors were the daily maximum current speed [m.s^{-1}], daily salinity range and inundation time [% in this example]. The black line represents the 1:1 ratio, quantiles 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

3.4 Optimal ecological niche

3.4.1 Quantile Regression with Gaussian equation

The modelled responses for each ENM quantile are represented by a projection on one axis per predictor with the observed data to observe the univariate effects of each variable (Figure 4 A1 & B1). The observed distribution of cockle biomass was left skewed, with a majority of records at low biomass values, and rare high biomass values, reflecting the validity of the choice of QR models. In addition, records were observed all along the environmental gradients of the selected predictors. The maximum observed responses located above the upper envelope of the model at τ=0.975 are close to the model optimum. Furthermore, the two models can clearly be applied without any preference in terms of robustness, given the performance shown by the predicted/observed graph (Figure 4 A2 & B2), where we can see that the 97.5th percentile has a slope of 1 and a high R^2 in both models. The models using density showed the same results (Supp. Data 3.4.1). The coefficients of the models are displayed in Table 4, and optimum for each model is described in the range of predictors encompassing the realised biomass:

A. Daily maximum current speed [m.s^{-1}] & daily salinity range & inundation time [%] (Figure 4 A1 & A2): The optimum was of 167 gAFDW.m^{-2} at 0.48 m.s^{-1}, with a range of 3.16 unity of salinity and 100 % inundation time. The optimum niche is a low intertidal zone with calm waters, where salinity is quite stable.

B. Daily maximum current speed [m.s^{-1}] & inundation time [%] & mud content [%] (Figure 4 B1 & B2): The optimum was of 239 gAFDW.m^{-2} at 0.43 m.s^{-1}, 100% inundation time and 31% of mud content. The optimal niche corresponds to low intertidal zones, with calm waters and muddy sands sediment.

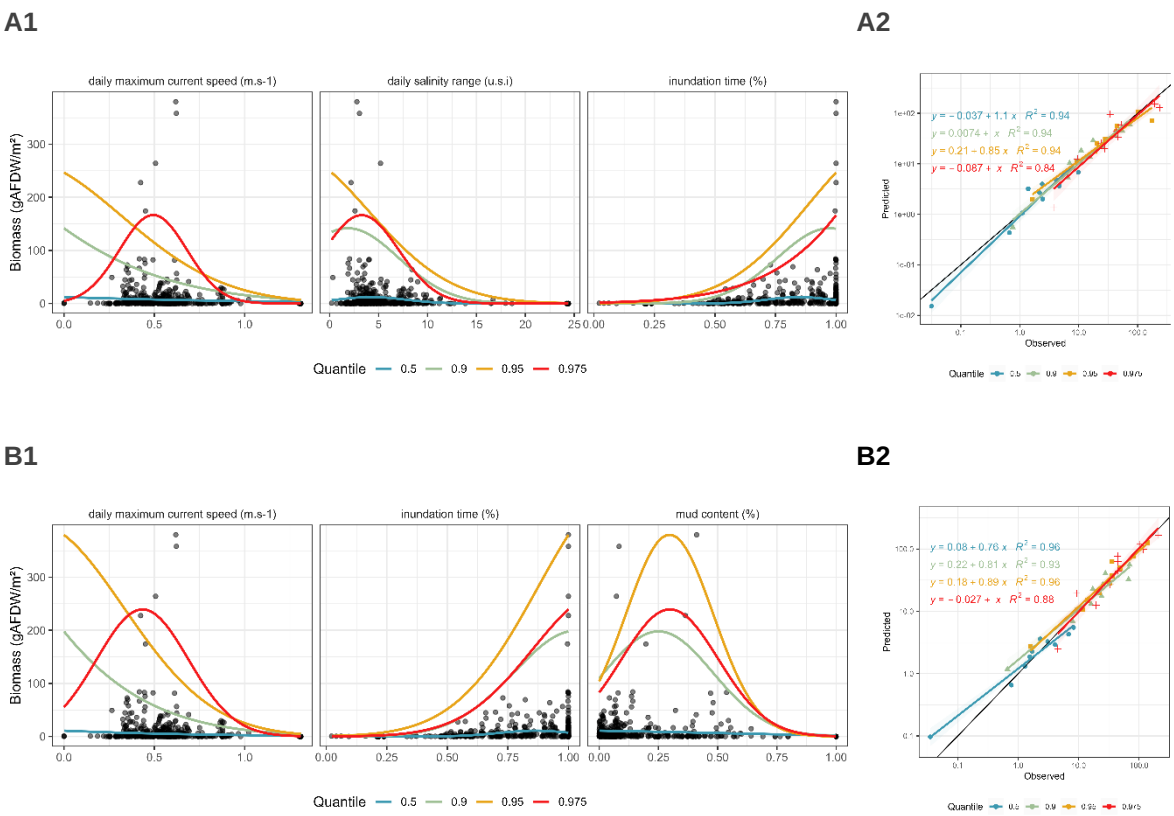


Figure 4: First row – (%) Projection on the three abiotic factor axes with observation compared to the modelled quantiles for the daily maximum current speed (m.s-1), the daily salinity range and the inundation time (A1). The second column displays the predicted/observed validation plot associated to this model (A2). Second row – Same figure with the 2nd model with projection on the three abiotic factor axes: daily maximum current speed (m.s-1), inundation time (%) and mud content (%) (B1); The second column displays the predicted/observed validation plot associated (B2). Black dots in A1 and B1 represents the observed data; lines the modelled quantiles; Coloured dots in A2 and B2 correspond to each decile of the modelled distribution and its corresponding observed, black line represents the 1:1 ratio. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

$$= A.e^{-\left[\frac{(Predictor1-\mu1_\tau)^2}{2.\sigma1_\tau^2}+\frac{(Predictor2-\mu2_\tau)^2}{2.\sigma2_\tau^2}+\frac{(Predictor3-\mu3_\tau)^2}{2.\sigma3_\tau^2}\right]} \quad (1)$$

Table 4: Coefficient of the models computed with gaussian equation (Equation 1), by quantile and response.

	Biomass (gAFDW/m²)							Density (ind/m²)						
tau	A	μ 1	μ 2	μ 3	σ 1	σ 2	σ 3	A	μ 1	μ 2	μ 3	σ 1	σ 2	σ 3
daily maximum current speed (m.s-1) * daily salinity range (u.s.i) * inundation time (%)														
0.50	41.55	-2.89	4.26	0.85	1.84	3.51	0.13	9,509.94	-2.24	5.94	0.81	0.93	3.57	0.18
0.90	716.49	-1.87	1.87	0.97	1.04	5.18	0.22	2,686.24	0.17	4.37	0.95	0.31	4.41	0.21
0.95	392.63	-0.26	-4.40	1.22	0.58	8.40	0.34	113,728.75	0.39	5.24	3.30	0.24	3.62	0.86
0.975	3,464.31	0.49	3.27	2.69	0.19	3.79	0.69	421,906.57	0.48	-21.93	2.95	0.19	14.63	0.80
daily maximum current speed (m.s-1) * inundation time (%) * mud content (%)														
0.50	80.54	-3.06	0.86	-0.28	1.56	0.15	0.71	292.75	0.33	0.79	0.27	0.19	0.17	0.35
0.90	1,321.22	-1.76	1.03	0.25	0.90	0.26	0.23	7,495.16	0.42	2.26	0.43	0.20	0.86	0.27
0.95	491.99	-0.17	1.22	0.30	0.50	0.34	0.18	85,227.47	0.46	4.01	0.62	0.20	1.20	0.48
0.975	272.78	0.43	1.15	0.30	0.25	0.30	0.20	151,774.30	0.50	4.77	0.41	0.21	1.40	0.32

3.4.2 Spatio-temporal variations of habitat suitability

The Optimal Ecological Niches, QR ENM with the Gaussian equation, were standardised on the basis of the model optimum at the 97.5th percentile, to obtain a value ranging from 0, an unfriendly environment for cockles, to 1, a very suitable environment, which makes it possible to simply assess the habitability potential of a geographical area. The OEN was applied geographically to define the habitat suitability of the different areas of the estuary on all periods defined. The suitability index, summary of the habitat suitability of each period and area is plotted to visualise differences in time and space (density in Supp. Data 3.4.2).

Daily maximum current speed [m.s^{-1}] & daily salinity range & inundation time [%]: The maps (Figure 5 A) showed that the channel and northern mudflats were the least favourable areas, the southern mudflats and offshore were more appropriate, but few locations were really optimum. The suitability index (Figure 5 B) ranged from 0 to 0.6 and was generally stable, confirming that the most suitable area was the southern mudflat followed by the offshore zone. The suitability of the northern mudflats increased after 2005, in particular the northern downstream mudflat. The salinity part of the model had a noticeable effect on the result of the model, and the increase of habitat suitability for cockles on the 3 northern mudflats can clearly be related to the decrease in the daily salinity range in these sectors.

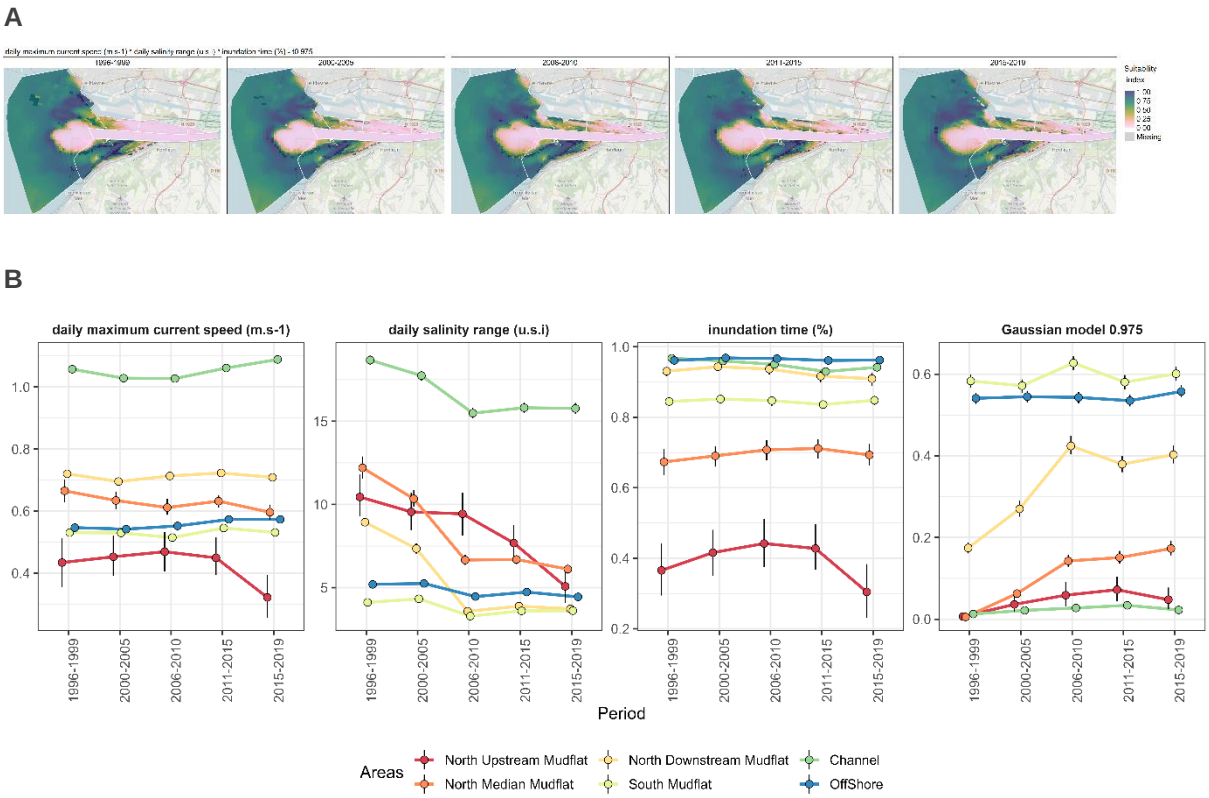


Figure 5: A: Daily maximum current speed [m.s^{-1}] & daily salinity range & inundation time [%] model suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile suitability index per period and per area for all SDM models with a 95% confidence interval.

Daily maximum current speed [m.s^{-1}] & inundation time [%] & mud content [%]: The closer to the mouth of the estuary, the higher the suitability; the offshore area had an advantage, which has deteriorated since 2011 (Figure 6 A). The apparent patchiness in the habitat suitability in the model results is linked to the spatial distribution of mud content (Supp data 3.2). The suitability index (Figure 6 B) varies from 0 to 0.5, with the highest value in the offshore area and the lowest in the channel. The offshore and the southern mudflat were similar in terms of suitability and are the most suitable areas, joined by the downstream northern mudflat over the last three periods. The northern upstream and median mudflats showed an increase in habitat suitability over the first three periods from 1996 to 2010. It is difficult to identify the contribution of one predictor over the others in explaining this trend.

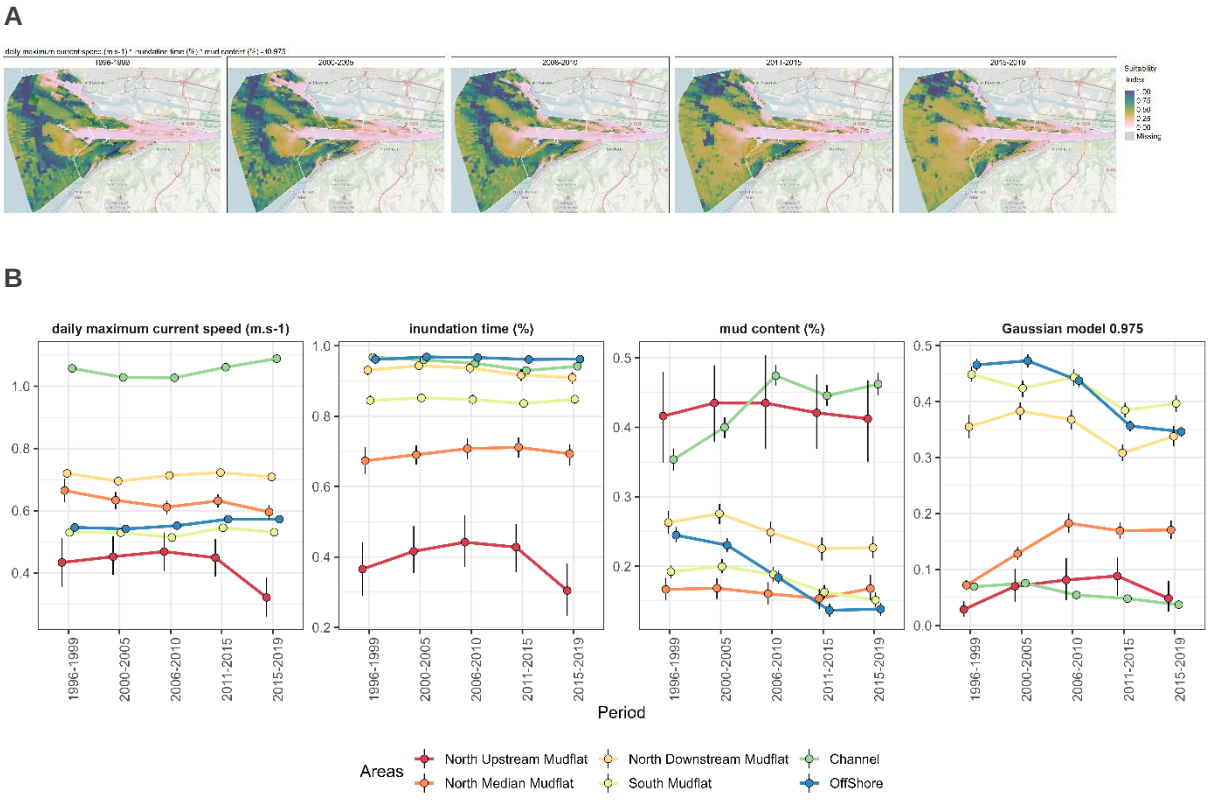


Figure 6: A: Daily maximum current speed [m.s^{-1}] & inundation time [%] & mud content [%] model suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile suitability index per period and per area for all SDM models with a 95% confidence interval.

3.4.3 Comparison and application to Scheldt basins data

The data from the Scheldt estuary was projected onto the Optimal Ecological Niche for the cockle defined in the Seine estuary using the daily maximum current speed [m.s^{-1}], daily salinity range and inundation time [%] model (Figure 7 A). The modelled response in the Scheldt was calculated by applying this OEN and the performance of the model is shown in Figure 7 B. The model fitted to the Seine data applied to the Scheldt is not appropriate at the 0.5 quantile, but is better simulated at the higher quantiles, with positive slopes reaching 0.71 at τ=0.95 and 0.67 at τ=0.975, (Figure 7 B). These

regression lines are relatively far from the diagonal, revealing that the model fitted to the Seine data is not very reliable when applied to the Scheldt basins.

When considering the scatterplots of observed biomass as function of the 3 descriptors (Figure 7 A), we can notice that the response to daily salinity range and the inundation time was different between the Seine and the Scheldt basins. The distribution of the recorded biomass as a function of the daily salinity range is difficult to compare, because the present day Oosterschelde basin only receives minor freshwater inputs, unlike the Westerschelde and thus lacks a full salinity gradient. With regard to inundation time, there are also discrepancies between the fitted model and the data recorded in the Scheldt basins, where the best optimal habitat was located on the foreshores with ~50% of the inundation time, whereas this modelled ENM was predicted at values of 100% of the inundation time. As for the maximal current speed, the model appeared to be a better fit, but the highest realized cockle's biomass was observed at a slightly lower current speed (~0.4 $m.s^{-1}$) even though the difference is within the error of the numerical model (pers. com. Smolders).

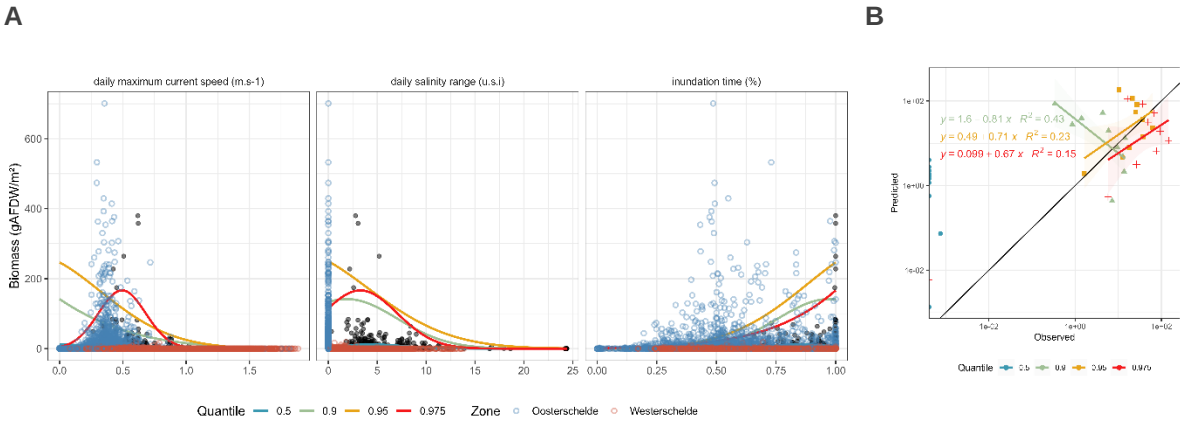


Figure 7: Seine model daily maximum current speed ($m.s^{-1}$) & daily salinity range & inundation time (%) projection on the three abiotic factor axes with data from Scheldt basins in blue dots for Oosterschelde and red dots for Westerschelde (A) and the predicted/observed validation plot computed on Scheldt application of the model parametrized in the Seine estuary (B). Black dots in A represents the observed data that were used for parameterisation (in the Seine estuary) while green dots are the data from the Scheldt basins; lines represent the model quartiles. Coloured dots in B correspond to each decile of the modelled distribution and its corresponding observed, black line represents the 1:1 ratio. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

4 Discussion

4.1 Optimal ecological niches for cockles

In line with previous knowledge, our study identified current velocity, salinity fluctuations and inundation time as main environmental drivers of cockle distribution. We can emphasize that the proposed model which combines the effect of those three factors can be considered valid and robust, both for biomass and density of cockles, at least in the Seine estuary. This model especially focusses on the influence of hydrodynamic forcings generated by the tides and the fluvial regime and the morphology of the estuary, which generates shallow and intertidal areas. Under these conditions, salinity

increases with water depth, as it represents the upstream-downstream gradient of the estuary, and the lower the inundation time, the greater the mixing between fresh and marine waters. The optimum given by this model corresponds to low shores (typically the offshore zone with 100% of inundation time), without intense variation in salinity (daily range of ~3), in sectors subjected to relatively strong currents (~ 0.5 $m.s^{-1}$). The position on the shore, related to inundation time, must affect the suspension-feeding periods on phytoplankton and also probably the periods when cockles are accessible to predators (Cozzoli et al., 2014). Low inundation time must therefore encourage both survival and growth, mainly related to prey-predator interactions. Regarding the effect of salinity, cockles are often reported to be negatively affected by fresh water supply and salinity rapid shifts are often described as responsible for mass mortality events in cockles, mainly linked to flash floods (Matos et al., 2023). The selection of these predictors agrees well with conclusions of other studies proposing SDM for *Cerastoderma edule* as this was the case in the Scheldt basins, Netherlands (maximal current speed and inundation time – Cozzoli et al., 2014), or the Aveiro lagoon in Portugal (where the predictors contributing the most in the definition of the ENM was salinity, submersion time and current velocity – Matos et al., 2023). Observations in cockle habitats of the British Isles were also in the same direction since the authors mention that cockles were unable to settle in calm waters (Boyden and Russell, 1972) and that the influence of tidal flow was found to be greater than that of salinity, the latter being an indirect indicator of the first and partially redundant.

A second alternative model combining the same predictors but with mud content instead of salinity range provide the same level of confidence in terms of robustness of the predictions. We proposed two versions of model to guarantee the best level of transferability and inter-comparison potential with future studies. We must mention, that, to our knowledge, this the first ENM proposed for cockles including mud content. The presence of mud has often been reported to play an important role in cockle performances and spatial distribution. Muddy-sand to sandy-mud sediments are often described as the best optimal habitat for cockles' recruitment and survival, as they provide a perfect balance between oxygenation and microphytobenthos as food supply (Bouma et al., 2001). For instance, in Portuguese lagoons, depth and average sediment grain size were the factors that better explained the probability of species occurrence (Santos et al., 2022). In fact, there must be a relative trade-off between two threatening constraints. On one hand, the absence of mud can clearly be related to strong currents provoking regular mud resuspension in the water column as well as the absence of microphytobenthos as food sources, while, on the other hand, a too intense presence of mud in sediment beds must make increase the vulnerability risks of cockles to eutrophication phenomena (anoxic conditions, contaminant presence). Cockles seem to be able to live in a broad range of habitats with a preference for mixed sediments, and more especially fine sands with a little proportion of mud. The distribution of biomass records across the diversity of sedimentary habitats in the Seine estuary display long distribution tails reaching 0% or 100% of mud content. This result is in agreement with previous observations in other ecosystems. For instance, this bivalve can show a preference for muddy bottoms in Netherland's estuaries, but can also inhabit sediments with a median grain size ranging from 50 µm (fully cohesive) to 250 µm (fully non-cohesive) (Cozzoli et al., 2013). Furthermore, the increase in mud content must also be related to the proximity of river discharge in many ecosystems (with correlation with salinity decrease). This is one

reason that we made the choice of one factor or the other in the 2 alternative models. The results are not exactly the same in terms of habitat suitability maps, but both versions generally converge.

In a previous study using QR, a SDM for cockles was proposed with only two predictors, the maximal current speed and the inundation time in the Scheldt basins (Cozzoli et al., 2014). They observed that the optimum was found in a medium intertidal zone (~50 % of inundation time) with a maximum current of ~0.5 $m.s^{-1}$. So, there is discrepancy between their conclusions and the one of the present study, especially when describing the role played by the inundation time. However, we must mention that, for the dataset of the Scheldt basins, the samples in the subtidal area were discarded because of methodological differences. This choice could explain a part of the contrasting conclusions, since we can have doubts if subtidal zones are really not occupied by cockle populations in the Scheldt basins. It is also possible that because of contrasting conditions (slope of the cross-shore, hydrodynamic conditions or morphological landscapes…), the settlement preference can occur either at the minimum limit of the intertidal shore as observed in the Seine or in the middle position of intertidal shores, as observed in the Scheldt basins. This is unlikely that these contrasting preferences derive from genetic differences between populations, since studies investigating the genetic patterns of cockles in Europe suggest a common genetic sub-population with a northern group globally consisting of the northern North Sea (Vera et al., 2023). These contrasting findings must rather be related to historical processes and local adaptation of cockle populations, despite the high level of larval connectivity across northern North Sea.

In another study located at the Ria of Aveiro in Portugal, the optimal habitat was observed for calmer conditions (~0.2 $m.s^{-1}$) compared to our results, but the most suitable habitat was found in similar conditions to our results regarding inundation time and salinity, since they found increasingly suitable conditions with the increase of salinity and submersion time (optimum for subtidal and marine waters). So, there could be a shift in current velocity and submersion time in the definition of the most suitable habitat, depending on the ecosystem. Even if, this time, genetic diversity can partly explain some biological differences (Vera et al., 2023), since the genetic structure of cockles is clearly different between South Portugal and North Sea areas, we can suppose that the biological response to tidal currents can be relatively broad for cockles, generally, and could shift depending on the local environment. Apparently, cockles do not like still water at all in any ecosystem, and they clearly prefer locations with dynamic waters everywhere. Globally, there is a general consensus that cockles appreciate habitats located between the lower limit of the intertidal-subtidal shores and mid-shore positions, but cockles can prefer either the lower limit between intertidal and subtidal zones (as in the Seine estuary), while they can prefer the central intertidal shores in other places as in the Scheldt basins.

A more detailed analysis of the contrasting conditions between the Westerschelde, Oosterschelde and Seine basins reveals obvious divergences that preclude the definition of a generic optimum for cockles, reliable everywhere. In particular, the Oosterschelde is a virtually closed basin with little freshwater input, whereas the Seine and the Oosterschelde are open estuaries. These discrepancies clearly indicate that the optimal conditions for cockles are indeed different in the three basins, and especially in the Oosterschelde. These conditions lead to different covariance structures for the physical

609 factors, but do not call the model into question, although not all conditions present in the Oosterschelde
610 are represented in the Seine data. The upper boundary models cannot really extrapolate to new
611 conditions, but they can be successfully applied to new scenarios under the boundary conditions of the
612 training data set. In general, the Oosterschelde, which is not influenced by freshwater input and has
613 calmer waters, represents the best optimal habitat in this system, unlike the Seine or the Oosterschelde.

614 Questions can also be raised about the number of predictors to be retained in the ENM for cockles
615 and the level of complexity to be retained. First, it is possible that among the three predictors of the two
616 models we propose, there is one that contributes less and could be removed, or that does not shed light
617 because of its redundancy with another more structuring factor. By testing the fit of the QR models with
618 different combinations of predictors, the results were clearly less well predicted with only two descriptors.
619 Of all the physical factors, we are relatively confident in the selection of the predictors we decided to
620 retain, namely maximum current velocity, inundation time and a third predictor (either salinity or silt
621 content).

622 It seems unlikely that the addition of descriptors extractable from hydrodynamic 3D model could bring
623 improvements, in terms of validation or model quality. However, the role of food availability and
624 especially the chlorophyll concentration in the seawater must be relevant for these suspension-feeders.
625 For instance, the study in the Ria of Aveiro (Matos et al., 2023) retained chl *a* concentration as well as
626 nitrate concentration as secondary predictors. In the Wadden sea (Netherlands), the residual of a SDM
627 show some correlation level with chl *a* concentration, suggesting a potential improvement by adding this
628 predictor (Folmer et al., 2017). In Baie des Veys, in Normandy (France), a study focused on the coupling
629 between benthic and pelagic components had also identified that the best correlated variable to cockle
630 biomass was the pelagic chl *a* concentration even if this chl *a* was more related to resuspended
631 microphytobenthos to phytoplankton in this case (Ubertini et al., 2012). The abundance of
632 microphytobenthic biofilms, especially high in sand-mud mixtures (Morelle et al., 2020) and their
633 resuspension rates must be very relevant as a food supply for cockles (Rakotomalala et al., 2015;
634 Sauriau and Kang, 2000; Ubertini et al., 2012). This addition of chl *a* concentration and trophic predictor
635 could be modelled by incorporating a biogeochemical model coupled to a 3D hydro-sedimentary model.
636 Unfortunately, this kind of biogeochemical models are not so easily available everywhere. In an attempt
637 of exploring a ENM that could be transferred to other systems, it seems essential to consider food
638 limitation and carrying capacities of the ecosystems in terms of phytoplankton or microphytobenthos.
639 Herman et al. (1999) clearly showed a dependence of system-averaged benthic biomass on the
640 magnitude of the spring phytoplankton bloom and there is a clear dependence of macrozoobenthic
641 biomass and especially that of suspension-feeders on primary production rate when comparing different
642 ecosystems. For instance, the fact that cockles biomass is very low in the Westerschelde compared to
643 the Oosterschelde, can be clearly explained by the primary production level that can exceed ~ 300 $gC.m^{-2}.y^{-1}$ in the Oosterschelde, with a factor of 3 higher than in the Westerschelde (Herman et al., 1999). In
645 the Seine estuary, the recent estimate of primary production provides the value of 65 $gC.m^{-2}.y^{-1}$ (Morelle
646 et al., 2018). There is also a possibility to improve predictions of ENM of benthic bivalves by including
647 other biotic variables, as observed in New Zealand where the inclusion of co-occurring species improves
648 the prediction quality by integrating ecological theory about species interaction (Stephenson et al.,

2022). However, increasing the level of complexity too much is not necessarily a model improvement, since there a lot of redundancy and correlation among variables, when adding several predictors that could interplay.

4.2 Assessment of the methodology

The construction of an ENM using QR makes it possible to define an OEN, i.e. the optimal biological development in a given ecosystem. This involves defining the environmental conditions for which the highest biomass is possible according to a defined set of factors. This approach differs from an AM approach, where the maximum number of available factors is used to define a species distribution model. Simplifying the environment to a limited number of factors makes it easier to apply and transfer the niche to other environments, allowing comparisons between different locations. QR models could not only be used to detect heterogeneous effects of descriptors at different quantiles of the biological response, but also offer more robust and comprehensive estimates compared to mean regression, when the normality assumption is violated or if there are outliers or long tails of the distribution. These advantages make QR attractive, particularly if they are extended to apply independent datasets (Huang et al., 2017).

By comparing the recorded data with the niche modelling, it is possible to assess its biological and physiological relevance. We chose to use a Gaussian equation to rigorously link the biological response to abiotic factors, based on current knowledge and classical distribution law reliable for biological populations in response to any environmental factor. This type of equation has the advantage of obtaining a unimodal response, unlike what can be obtained with a B-spline at the third degree, for example. This choice avoids retaining a model that seems quite good in terms of adjustments, but which simulates unfounded distributions. In addition, the niche model thus obtained is a continuous response, i.e. with no tipping point towards an unfavourable state, the biological reality of which is debatable when the selected factors are considered, in an estuarine environment defined by gradients and strong variations in abiotic conditions.

On the other hand, the QR approach makes it possible to respond to the very local effects and natural patchiness that can affect biological populations and lead to very high densities of a species in a local 'patch', a phenomenon often observed in estuarine environments. Community self-organisation takes place at several overlapping spatial scales, strongly expressed by tidal constraints, where micro-scale organisations are able to create micro-climates 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 aim of this study was to define the HMS conditions most favourable to the development of a species, and not necessarily the niche representing the most exceptional circumstances, hence the choice of a high but not necessarily maximum quantile. The very high quantiles correspond to the niche that reflects the biological observations resulting from the patchy distribution of species. Species distributions and the inherent patchiness can be studied in details on the basis of the maximum density of intertidal species, for instance (Thrush et al., 2003).

Whatever the model used, the quality of a SDM depends first and foremost on the reliability of the input data. The Seine 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. The succession of generations in a population in an evolving ecosystem is key information for understanding the dynamics of a population in its environment. With regard to environmental data, the abiotic field data, synchronous with the biological data, are susceptible to highlight very small atypical habitats rather than macro-spatial trends. The use of a hydro-morpho-sedimentary model therefore makes it possible to better describe the overall “smoothed” environment, with a large scale.

However, the synthesis of abiotic data, which is generally available at much higher frequencies than biological data, is subject to choices that have an impact on the way in which the niche is interpreted. In this study, the abiotic data are summarised at their annual median (over a hydrological year, from October to September) and aligned with the biological samples, so that they represent the recent history of the individual sampled. The long time series (at least 2 decades) then makes it possible to represent an ecosystem in which we find a fauna that is subject to this local climate, which may or may not evolve over generations.

In intertidal environments, the interactions between an environment and its biotope are part of a feedback loop: organisms are adapted to certain abiotic conditions, but they are able to significantly modify certain key abiotic parameters that define their environment, in particular sediment erosion parameters via bioturbation (Kristensen et al., 2012). Cockles, for example, are known eco-engineers that can modify their environment, in particular sediment content (Donadi et al., 2014, 2013). They modify their habitat to obtain better conditions (Li et al., 2017) and interact strongly with the microphytobenthos, creating biofilms that modify the erodibility of the sediments (Eriksson et al., 2017; Ubertini et al., 2012). These bioturbation processes are not yet included in HMS models, even though they can have a significant impact on estuary morphology (Orvain et al., 2012). Including these biota-mediated erodibility factors in HMS models may therefore have mitigating effects on the long-term evolution of habitats (Lehuen et al., 2024), and this should significantly improve the prediction of abiotic factors and their use for defining ENM/SDM. The aim is to better integrate the local effects exerted by benthic fauna (in particular bioturbation) into complex large-scale interactions in order to consolidate long-term projections.

Moreover, the ENM obtained applied in SDM is not capable of predicting a drastic change in population that would be subject to short episodes of stressful events. In particular, constraining episodes occurring in the context of climate change could become a threat to the future of a population, leading to drastic changes in community succession initiated by a long-term change in physical conditions (Baltar et al., 2019). Examples include heat waves or highly erosive storms, the duration, intensity and frequency of which can affect the recruitment and development of populations. This is where the long-term climate approach comes up against its real limit: the representativeness of climate variability and the question of event frequency, which is the key to understanding the effects of climate change that could lead to a shock to biodiversity or productivity. Extreme events are insufficiently defined

by a simple maximum of environmental values, as this has been demonstrated experimentally for the case of heat waves (Zhou et al., 2022).

Abiotic data from HMS models can be used to describe complex patterns between the main physical factors, but the evolution of ecosystems in response to climate change may lead to previously unconsidered parameters becoming critical parameters for biological development, such as pH. Indeed, the acidification of marine waters is an identified consequence of their warming, and its impact on bivalves' organisms has been demonstrated (Thomas and Bacher, 2018). There are experimental studies on the biological response to ranges of variation in temperature, salinity or 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, in environments such as the Seine estuary, pH is not traditionally considered to be an environmental factor that plays an important role in the distribution of species at least during the past survey planning.

Taken together, all these limitations justify recommending a cautious interpretation of the use of niche models in extrapolative and long-term projections. Indeed, by defining an average trend in the evolution of HMS factors in the estuary in order to assess the future of a species, this exercise could completely miss the dangers encountered by the population studied and provide erroneous information, whether reassuring or alarming.

4.3 A tool for ecosystem management

ENMs and their SDM application are tools that can effectively be used for the management of natural areas, highlighting the spatio-temporal differences in a given territory according to selected factors. In this case, the model can be used to monitor the potential productivity of target species, to ensure that the presence of a population that provides the ecosystem services required by the estuary is facilitated. ENM/SDM can also be used to monitor the progress of an invasive species in a territory (Srivastava et al., 2019), measure the impact of anthropogenic structures (Cozzoli et al., 2017), or define a conservation strategy for an endangered species (Frans et al., 2022).

The use of an ENM in a given space depends on the technique used. Existing SDMs using the AM approach provide high-performance SDMs, but it is not possible to apply them to the data set available to us. This led us to choose the QR ENM method, which provides a set of equations based on a reasonable number of factors that are generally accessible in the context of managing an ecosystem such as an estuary.

As seen in the previous paragraphs, the ENM obtained and its application in SDM makes it possible to control a geographical area such as an estuary in the medium term (~10 years). However, in this study we would rather not project the niche into a future environment to avoid any speculation, as it would probably not be able to respond to distant horizons for which the environment would be more significantly modified. The tool nevertheless remains operational in a context of management of a natural area subject to anthropogenic pressure, simply illustrating the zones favourable to the cockles. The

habitat suitability model also makes it possible to identify any drift in the areas of interest, and to begin a diagnosis of the causes of this drift, by adapting the temporal and spatial resolution as required. In fact, as the SDMs are linked to the HMS variables, the habitat suitability is a good indicator of the potential levers for dealing with changes in ecosystems, in particular due to human activities, as well as the effects of global climate change.

The results of this study showed, for example, an improvement in the habitability of cockles on the intertidal mudflats of the Seine, due to the saline intrusion already obvious. This trend should continue in the future for cockle, but at the expense of the more euryhaline species that typically colonise intertidal mudflats further upstream, such as *Hediste diversicolor* or *Scrobicularia plana*. However, increasing salinity can be accompanied by a reduction in freshwater input, which can lead to a limitation in nutritive salts and therefore in primary and secondary productivity, resulting in a risk of population declines and a global rarefaction of benthic communities, whatever the niche.

The ENM/SDM are generally developed for an isolated species, but the management of a natural area requires an approach not only on a broad spatio-temporal scale, but also on the scale of species communities and the ecosystem services that we wish to maintain. The biodiversity approach using the Shannon index has been used in an SDM (Cozzoli et al., 2017). In another way, the introduction of inter-species interactions has been explored in the form of an explanatory biological factor in an SDM (Stephenson et al., 2022), which improves the model but reveals complex interaction patterns as soon as two species are studied. In addition, we can envisage modelling the biological response of a species community according to a set of environmental variables, in order to represent the complete biotic environment, as initiated in the Wadden Sea (Folmer et al., 2017). However, defining a community of species is very closely linked to the analysis prism chosen. Depending on the question raised, it will be relevant to construct a community according to life traits, functional traits - trophic, bioengineering -, the food web or the ecosystem services that the macrofauna can provide.

5 Conclusion

Because of their complex structure and strong gradients, understanding estuarine ecosystems can benefit from modelling the ecological niches of its fauna using ENM and SDM tools. The extraction of physical descriptors from 3D HMS models of water and sediment transport and the method of describing ecological niches using quantile regression enabled a detailed analysis of the environmental needs of the cockle. The two models built in this study, QR ENM at the 97.5th percentile with a Gaussian equation, combining maximum daily current speed, inundation time and daily salinity range or mud content as a third predictive factor, provide a robust description of the cockle's optimal ecological niche. This niche, standardised in the form of habitat suitability, allowed a geographical visualisation of the habitability of the estuary for the cockle, as well as its temporal evolution by areas of interest. The application of one of the ENMs obtained to another estuary showed the potential for transferability, while revealing the need to define a niche with additional elements. In particular, it seems necessary to integrate trophic components and in particular the availability of microalgal resources (phytoplankton and microphytobenthos). Based on general theories concerning the relationship between primary and

secondary productivity, it seems relevant to incorporate a model simulating chl *a* into 3D models before being able to propose a truly generic and transferable ENM model. This could be debated, since the representation of the correlation between drivers (including food) could make the difference.

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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: Principal Components Analysis (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: Example of modelled vs observed biomass data plotted for each model functions. The selected predictors were the daily maximum current speed [$m.s^{-1}$], daily salinity range and inundation time [% in this example]. The black line represents the 1:1 ratio, quantiles 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

Figure 4: First row – (%) Projection on the three abiotic factor axes with observation compared to the modelled quantiles for the daily maximum current speed (m.s-1), the daily salinity range and the inundation time (A1). The second column displays the predicted/observed validation plot associated to this model (A2). Second row – Same figure with the 2nd model with projection on the three abiotic factor axes: daily maximum current speed (m.s-1), inundation time (%) and mud content (%) (B1); The second column displays the predicted/observed validation plot associated (B2). Black dots in A1 and B1 represents the observed data; lines the modelled quantiles; Coloured dots in A2 and B2 correspond to each decile of the modelled distribution and its corresponding observed, black line represents the 1:1 ratio. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

Figure 5: A: Daily maximum current speed [$m.s^{-1}$] & daily salinity range & inundation time [%] model suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile suitability index per period and per area for all SDM models with a 95% confidence interval.

Figure 6: A: Daily maximum current speed [$m.s^{-1}$] & inundation time [%] & mud content [%] model suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile suitability index per period and per area for all SDM models with a 95% confidence interval.

Figure 7: Seine model daily maximum current speed ($m.s^{-1}$) & daily salinity range & inundation time (%) projection on the three abiotic factor axes with data from Scheldt basins in blue dots for Oosterschelde and red dots for Westerschelde (A) and the predicted/observed validation plot computed on Scheldt application of the model parametrized in the Seine estuary (B). Black dots in A represents the observed data that were used for parameterisation (in the Seine estuary) while green dots are the data from the Scheldt basins; lines represent the model quartiles. Coloured dots in B correspond to each decile of the modelled distribution and its corresponding observed, black line represents the 1:1 ratio. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

Table list