Peer Community Journal

Section: Ecology

Research article

Published
2025-09-22

Cite as
Amélie Lehuen, Chloé Dancie, Florent Grasso, Sven Smolders, Francesco Cozzoli and Francis Orvain (2025) *A novel quantile regression approach to define optimal ecological niche: a case study on habitat suitability of cockle populations (Cerastoderma edule)*, Peer Community Journal, 5: e102.

Correspondence
amelie.lehuen@gmail.com

Peer-review
Peer reviewed and recommended by PCI Ecology,
https://doi.org/10.24072/pci.ecology.100678

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

Amélie Lehuen[1,2], Chloé Dancie[3], Florent Grasso[4], Sven Smolders[5], Francesco Cozzoli[6,7], and Francis Orvain[1,2]

Volume **5** (2025), article e102

https://doi.org/10.24072/pcjournal.630

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 habitat suitability index in this ecosystem was explored over a period of 25 years. 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.

[1] Marine Ecosystems and oRganisms reSEArch Lab, Esplanade de la Paix – CS 14032 – 14032 Caen Cedex 5 – France, [2] Université de Caen Normandie, Esplanade de la Paix - CS 14032 - 14032 CAEN Cedex 5 - France, [3] Cellule de Suivi du Littoral Normand, 53 rue de Prony, 76600 Le Havre - France, [4] Unité Dynamiques des Écosystèmes Côtiers, Implantations Ifremer : Arcachon, Brest, Dinard - France, [5] Flanders Hydraulics Research, Department of Mobility and Public Works, Flemish Government, Antwerp - Belgium, [6] Università del Salento = University of Salento [Lecce], Piazza Tancredi, 7, 73100 Lecce LE - Italy, [7] Research Institute on Terrestrial Ecosystems [CNR, Italy], Porano - Italy

CENTRE MERSENNE

Peer Community Journal is a member of the Centre Mersenne for Open Scientific Publishing
http://www.centre-mersenne.org/

e-ISSN 2804-3871

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 (Guisan & Zimmermann, 2000; Austin, 2002) and the mechanistic ones (Kearney & Porter, 2009), the latter being based on eco-physiological laws. Each approach has advantages and disadvantages (Kearney & Porter, 2009; Melo-Merino et al., 2020), but the vast majority of studies carried out to date are correlative (Robinson et al., 2011, 2017; Melo-Merino et al., 2020).

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 (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Franklin, 2010). 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 & Zimmermann, 2000; Van Der Wal et al., 2008; Melo-Merino et al., 2020).

Correlative SDMs encompass a multiplicity of statistical techniques, which can be divided into two approaches: algorithmic modelling (AM) and data modelling (DM) (Warren & 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 (Singer et al., 2017; Matos et al., 2023). 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 & 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 (Cade & Noon, 2003; Anderson, 2008). 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 & Herman, 2002) that may partly bias the biological response to a set of selected factor (Cade et al., 1999; Austin, 2007).

The use of quantile regression (QR) can counteract this limitation, by defining different quantiles of biological response depending on the abiotic factors chosen (Koenker & Machado, 1999; Koenker & Hallock, 2000). 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 (Cade et al., 1999; Cade & Noon, 2003; Cade et al., 2005; Austin, 2007; 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 & 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 (Herman et al., 2001; Chapman et al., 2010).

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 (Jones et al., 1994; Kristensen et al., 2012; Arlinghaus et al., 2021). 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 & 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 (Thrush et al., 2003, 2005; Anderson, 2008). 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 (Van Der Wal et al., 2017; Shi et al., 2020) 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 (Dauvin, 2015; Baffreau et al., 2017; Le Guen et al., 2019; Bacouillard et al., 2020) 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 (Schulz et al., 2018; Grasso et al., 2018, 2021; Grasso & Le Hir, 2019; Mengual et al., 2020). 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., 2013, 2014, 2017), 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 habitat suitability indices, as application of the normalized OEN, 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.

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.

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 1500 $m^3.s^{-1}$, 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 (Lesourd et al., 2003; Schulz et al., 2018; Grasso et al., 2021).

The mouth of the estuary hosts a variety of habitats that provide many ecosystem services (Boesch & Turner, 1984; Beck et al., 2001). 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 (Tecchio et al., 2016; Morelle et al., 2020) (Figure 1).

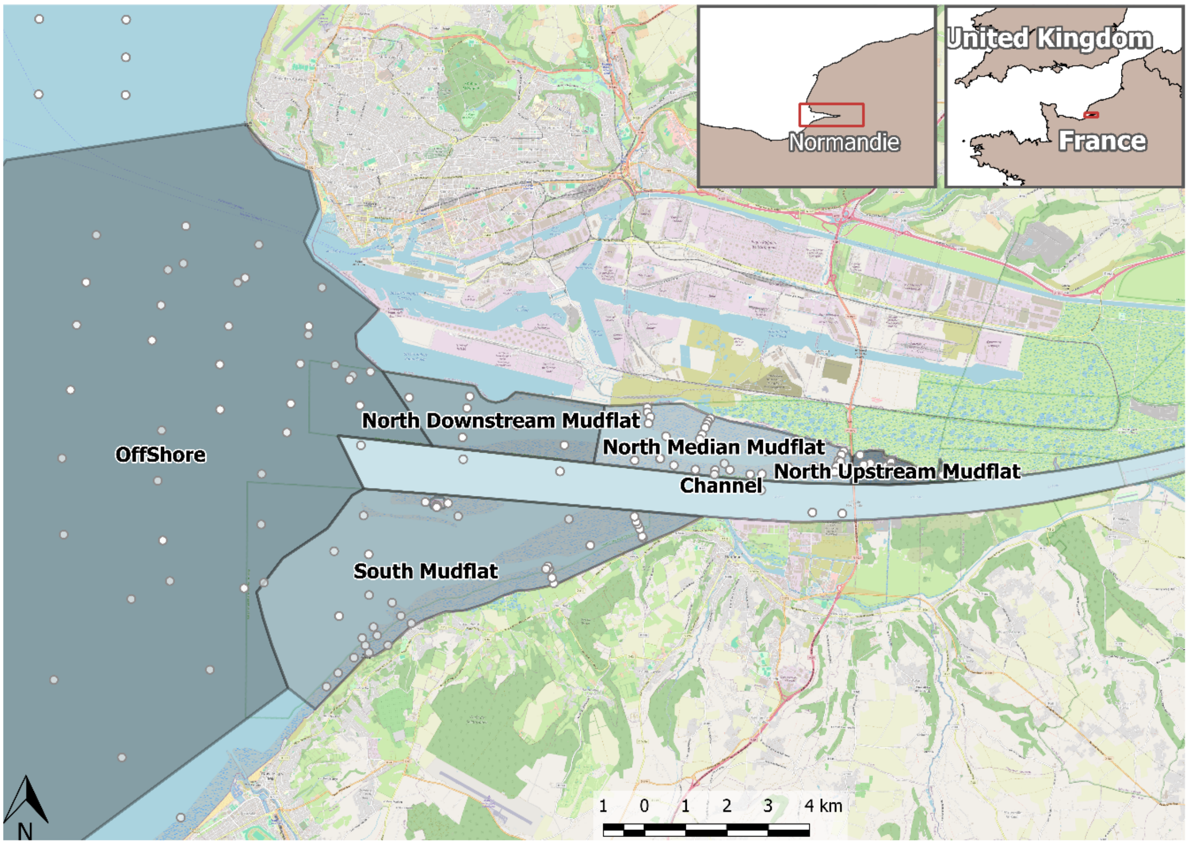

Figure 1 - Maps showing the habitats defined in the dataset of the study area. The dots represent the location of the biological samples of the dataset.

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 & 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 & 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) (Ubertini et al., 2012; Cozzoli et al., 2014). 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; Singer et al., 2017; Matos et al., 2023), salinity (Matos et al., 2023), temperature (Singer et al., 2017) and current velocity (Cozzoli et al., 2014).

Datasets

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 [$g_{AFDW}.m^{-2}$] – 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.

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 & 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 (Le Hir et al., 2011; Grasso et al., 2018; Mengual et al., 2020).

The HMS dataset was generated during the ARES project using the Mars3D model (Grasso et al., 2019, 2021). 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 & 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.

Model adjustments

Quantile regression

The mathematical theory of the quantile regression (QR) has been extensively expanded and described by Koenker over the past decades (Koenker & Bassett, 1978; Koenker & Machado, 1999; Koenker & Hallock, 2001; Koenker et al., 2024). Its use in ecological studies has increased since the first pioneering studies (Cade et al., 1999; Cade & Noon, 2003; Cade et al., 2005).

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]; 0.5 being the equivalent of an OLS regression, the other values higher than 0.9 to seek for the optimum response without risking overfitting of extreme values due to micro-geographical organisation.

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 habitat 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 habitat suitability index by area and period is calculated to visualise the global habitat 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)	$y_\tau = A.e^{-\left[\frac{(x1-\mu1_\tau)^2}{2.\sigma1_\tau^2}+\frac{(x2-\mu2_\tau)^2}{2.\sigma2_\tau^2}+\frac{(x3-\mu3_\tau)^2}{2.\sigma3_\tau^2}\right]}$ quantreg::nlrq (f (x1,x2,x3, initial.conditions)) Initial conditions: means (μ) and sd (σ) of each parameter	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))) Initial conditions: means (μ) of each parameter as on knot and degree 3	Avoid pre-determined shape of the equation and the use of a flexible non-linear function (Cozzoli et al., 2013)

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 R² developed by Koenker and Machado (Koenker & 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.

Results

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.

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. The current velocity has an impact on siphon aperture and filtration rates, indirectly regulating the growth performances (Jonsson et al., 2005). This factor also plays a role in the burrowing position, in relation to a fleeing behaviour face to strong currents, in order to avoid the erosion of the shell itself (Wiesebron et al., 2022). The process of the secondary settlement of the juveniles driven by current velocity is also well documented (De Montaudouin et al., 2003).

- 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. The tidal level defining the period of feeding of *C. edule*, it has a direct effect of growth rate (Richardson et al., 1980).
- 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. This parameter is a good indicator of the estuarine condition, and have shown a high impact on *C. edule* patterns (Matos et al., 2023). For adults individuals, low salinity response is valve closure, so less growth, and a stress that lead to less burrowing, as shown in (Domínguez et al., 2020; Verdelhos et al., 2021; Mahony et al., 2022).
- 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 mud content could affect *C. edule* habitability (Folmer et al., 2017), such as the processes of the secondary settlement of the juveniles (De Montaudouin et al., 2003). The bioturbation rate of cockles is also higher than in sand habitats, hence enhancing the disturbance of sediment erodibility (Soissons et al., 2019).

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.

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.

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.

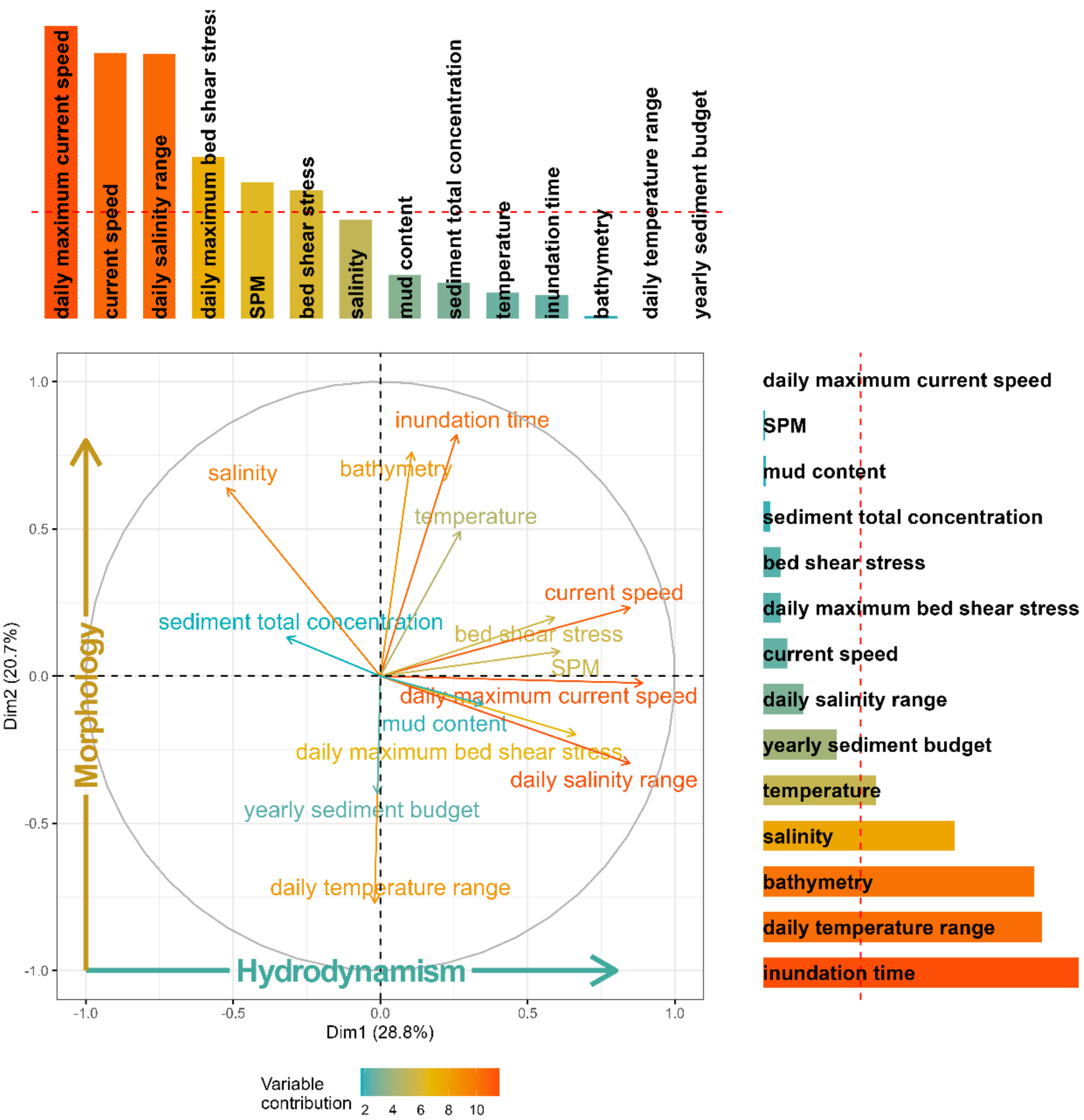

Figure 2 - Principal Components Analysis (PCA) variables correlation plot of the two main axes with the abiotic factors' contributions in bar plots for each axis. The colour of arrows and bars correspond to the contribution value of each variable. The red dotted line represents the mean contribution for all factors. The contribution of a variable to a given principal component is calculated as (Variable.cos2 * 100) / (total cos2 of the component).

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

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 observation of the validation plot (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 (g_{AFDW}/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

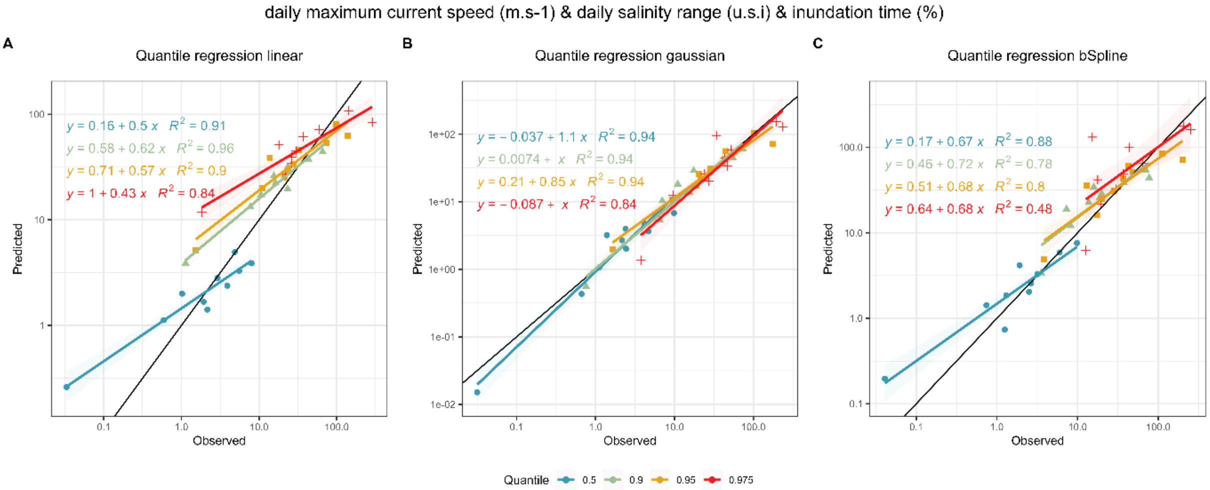

Figure 3 - Example of modelled vs observed biomass data plotted for each model functions. The predicted (model output) data were discretized in 10 homogeneous classes based on the predicted values and for each class, the correspondent sample quantile of the observed data was calculated. The selected 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, a linear correlation was drawn for each quantile between random-predicted and observed values. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

Optimal ecological niche

Quantile Regression with Gaussian equation

The modelled responses for each ENM quantile are represented by a projection on each 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 R² 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 observed biomass:

A. Daily maximum current speed [m.s^{-1}] & daily salinity range & inundation time [%] (Figure 4 A1 & A2): The optimum was of 167 g$_{\mathrm{AFDW}}$.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 g$_{\mathrm{AFDW}}$.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.

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

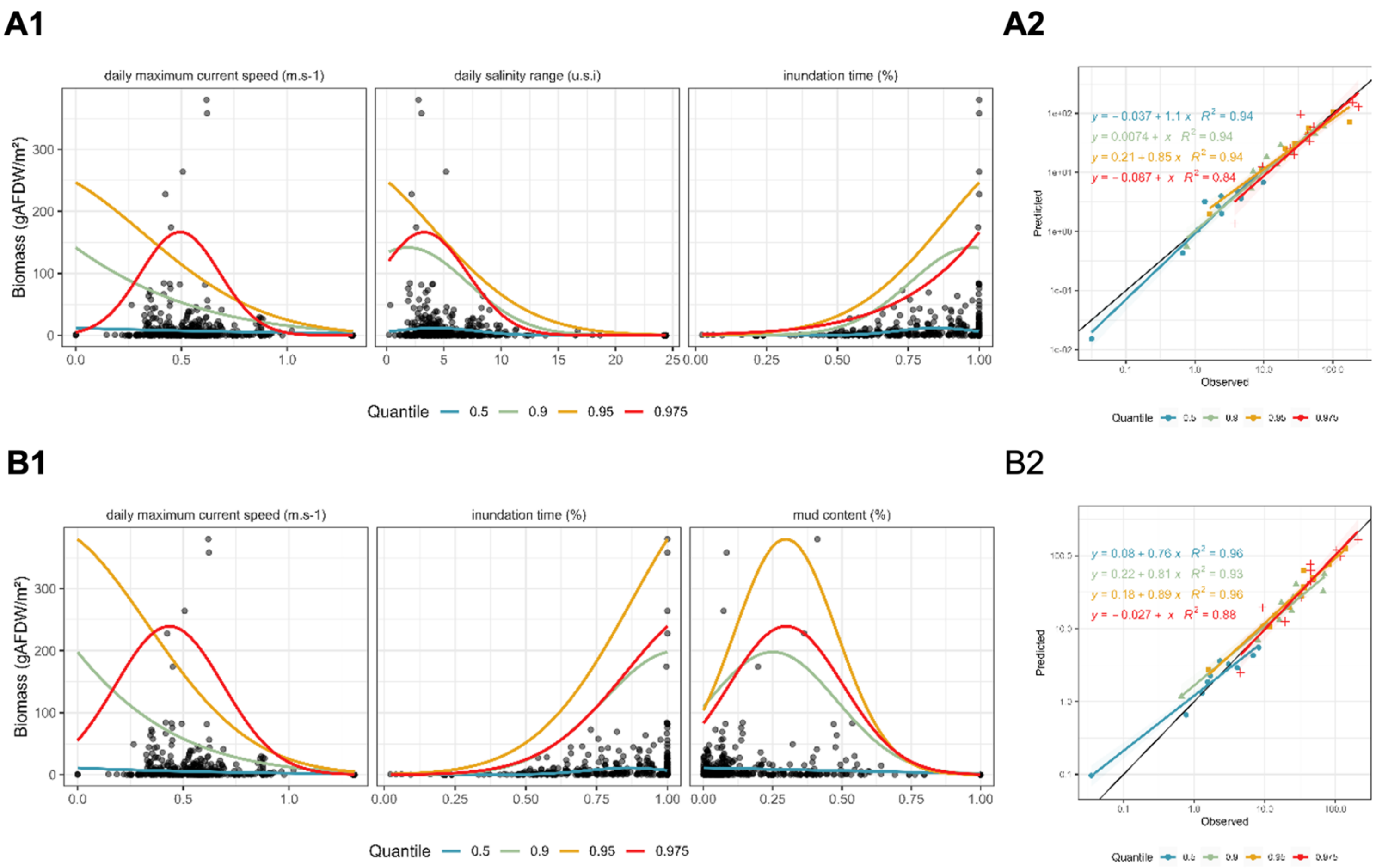

Figure 4 - The two Optimal Ecological Niches proposed. First row – (%) Projection on the three abiotic factor axes with observation compared to the modelled quantiles for the daily maximum current speed ($m.s^{-1}$), the daily salinity range and the inundation time (A1). The second column displays the 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; See Figure 3 for building of A2 and B2. Quantiles are colour coded as 0.5 in blue, 0.9 in green, 0.95 in orange and 0.975 in red.

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

	Biomass (g_{AFDW}/m^2)							**Density (ind/m^2)**						
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

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 habitat suitability 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 habitat 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 habitat 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 habitat 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.

Daily maximum current speed [$m.s^{-1}$] & inundation time [%] & mud content [%]: The closer to the mouth of the estuary, the higher the habitat 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 habitat 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 habitat 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.

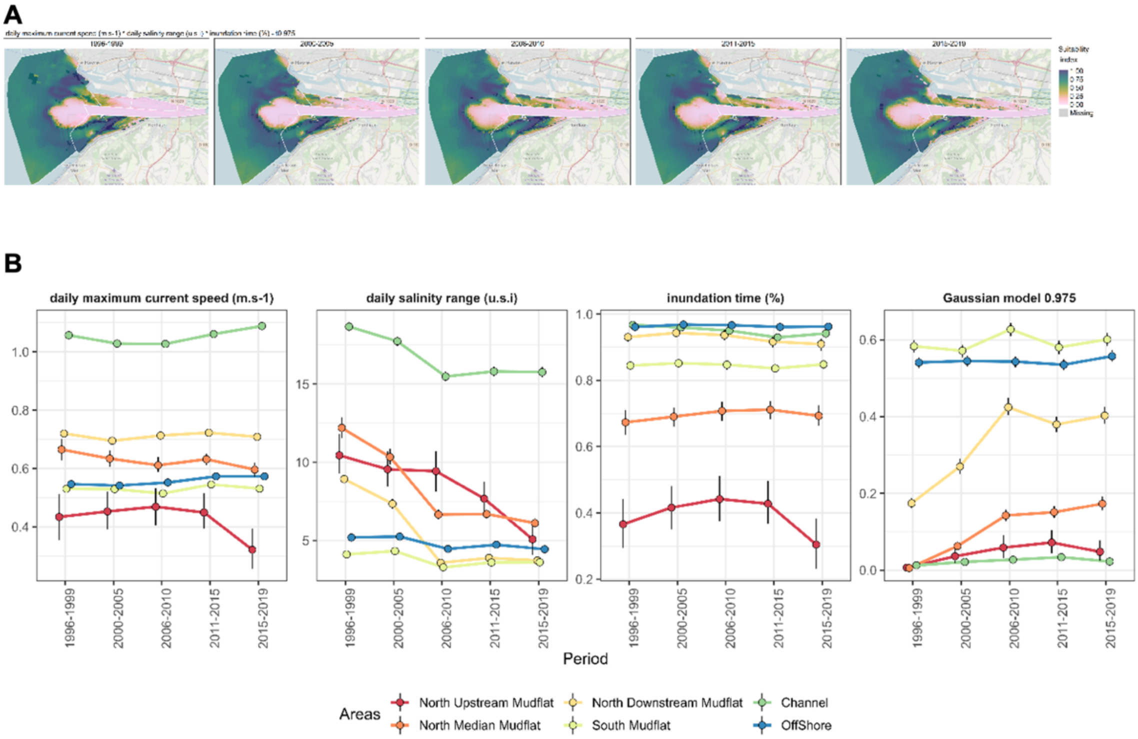

Figure 5 - A: Daily maximum current speed [m.s^{-1}] & daily salinity range & inundation time [%] model habitat suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile habitat suitability index per period and per area for all SDM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

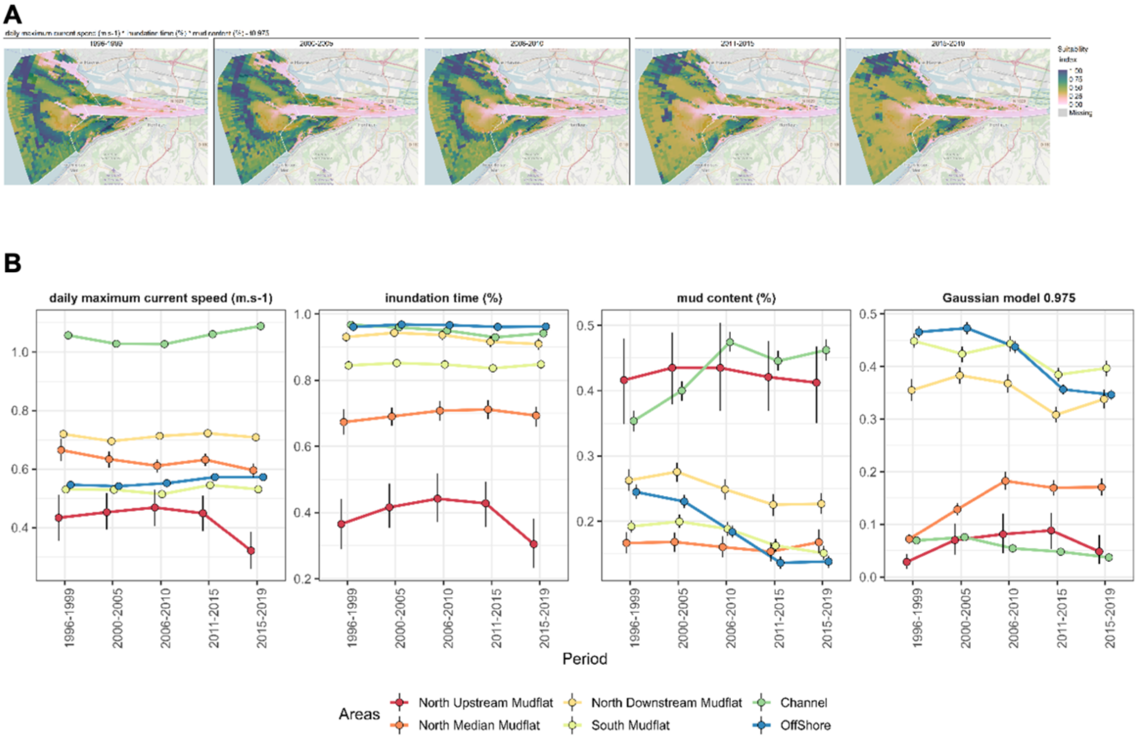

Figure 6 - A: Daily maximum current speed [m.s^{-1}] & inundation time [%] & mud content [%] model habitat suitability index applied on the Seine estuary over the five periods. B: Abiotic factors and resulting model at 97.5th centile habitat suitability index per period and per area for all SDM models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

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 observed 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).

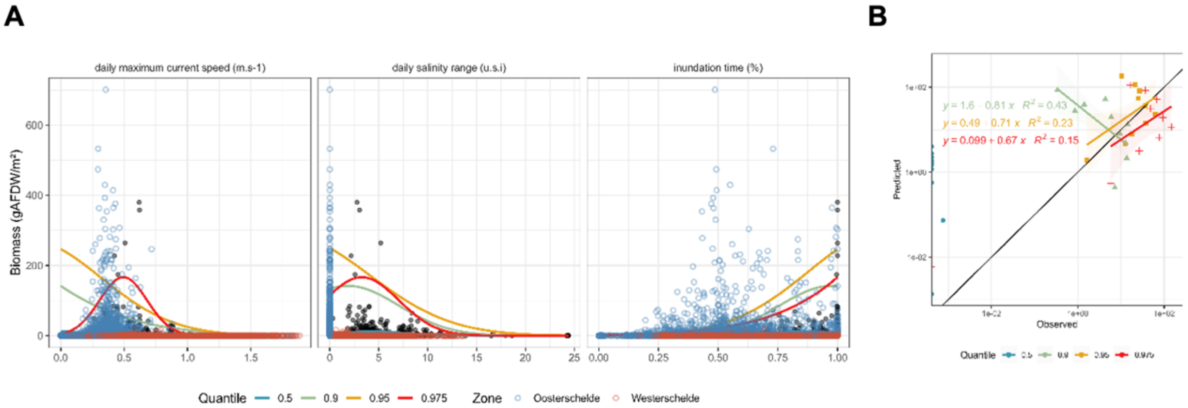

Figure 7 - Seine model daily maximum current speed (m.s^{-1}) & daily salinity range & inundation time (%) projection on the three abiotic factor axes with data from Scheldt basins in blue dots for Oosterschelde and red dots for Westerschelde (A) and the predicted/observed validation plot computed on 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. See Figure 3 for building of B, 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.

Discussion

Optimal ecological niches for cockles

In line with previous knowledge on cockle ecology, our study identified current velocity, salinity fluctuations and inundation time as the 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 variables of cockle populations, 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 & 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 regarding inundation time and salinity, since they found better suitable conditions with the increase of both 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 factors, but do not call the model into question, although not all conditions present in the Oosterschelde are represented in the Seine data. The upper boundary models cannot really extrapolate to new conditions, but they can be successfully applied to new scenarios under the boundary conditions of the training data set. In general, the Oosterschelde, which is not influenced by freshwater input and has calmer waters, represents the best optimal habitat in this system, unlike the Seine or the Oosterschelde.

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

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

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 (Underwood & Chapman, 1996; Ettema & Wardle, 2002; Thrush et al., 2005; Le Hir & Hily, 2005). 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 environment, at a wide scale and by disregarding very local spatial structures.

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 according to which the niche could be interpreted. In this study, the abiotic data were summarised at their annual median (over a hydrological year, from October to September) and aligned with the biological samples, so that they represented the recent history of the individual sampled.

In intertidal ecosystems, the interactions between the environmental context 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., 2013, 2014). 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 (Ubertini et al., 2012; Eriksson et al., 2017). 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 for the fate of cockle's populations, 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 acidification. Indeed, the acidification of marine waters is an identified consequence of the CO_2 partial pressure in the atmosphere, and the impact of the pH decrease has been demonstrated on bivalves' organisms (Thomas & 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 (Łapucki & Normant, 2008; Hale et al., 2011; Lemasson et al., 2017; Ong et al., 2017; Peteiro et al., 2018; Medeiros et al., 2020; Madeira et al., 2021). 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 exercises, scenarios of 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.

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). The tool nevertheless is very operational in a context of management of a natural area subject to anthropogenic pressure, simply illustrating the zones favourable to the cockles until now. 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 habitat suitability 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 describe a community by integrating life traits, functional traits – trophic features and bioengineering/bioturbation activities.

Conclusion

Because of their complex structure and strong spatial 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 SDM 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 habitat suitability 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.

Acknowledgements

The authors thank Tjeerd Bouma for his guidance and insight on the MELTING POTES project; Brian Cade for his precious help on quantile regression; The GIP Seine Aval, the Maison de l'Estuaire, the Cellule du Suivi du Littoral Normand and the Grand Port Maritime du Havre for the biological datasets; IFREMER for the Mars3D model dataset. Preprint version 3 of this article has been peer-reviewed and recommended by Peer Community In Ecology: https://doi.org/10.24072/pci.ecology.100678 (Goberville, 2025). The authors acknowledge reviewers for their valuable comments and suggestions.

Funding

This research was supported by the Region Normandie (A. Lehuen's PhD) and by the Office Français pour la Biodiversité (the MELTING POTES project).

Data, scripts, code and Supplementary data

Supplementary data, including data sources and Scripts are available in the same deposit of this article https://hal.science/hal-04438267 SDM Annx Data - Scripts.pdf for data sources and scripts, SDM_Suppl_Data.html for high resolution figures.

Conflict of interest disclosure

The authors declare they comply with the PCI rule of having no financial conflicts of interest.

CRediT author statement

A. Lehuen: Conceptualization, Methodology, Formal analysis, Writing - Original Draft, Funding acquisition ; F. Orvain: Conceptualization, Methodology, Validation, Resources, Writing - Review

& Editing, Supervision, Project administration, Funding acquisition ; C. Dancie: Resources, Data Curation, Writing - Review & Editing ; F. Grasso: Resources, Data Curation, Writing - Review & Editing ; S. Smolders: Resources, Writing - Review & Editing ; F. Cozzoli: Resources, Writing - Review & Editing

References

Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Anderson MJ (2008) Animal-sediment relationships re-visited: Characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *Journal of Experimental Marine Biology and Ecology*, **366**, 16–27. https://doi.org/10.1016/j.jembe.2008.07.006

Arlinghaus P, Zhang W, Wrede A, Schrum C, Neumann A (2021) Impact of benthos on morphodynamics from a modeling perspective. *Earth-Science Reviews*, **221**, 103803. https://doi.org/10.1016/j.earscirev.2021.103803

Aulert C, Provost P, Bessineton C, Dutilleul C (2009) Les mesures compensatoires et d'accompagnement Port 2000 : retour d'expériences. *Ingénieries-EAT*, **29**, 55–72. https://hal.inrae.fr/hal-02592496v1

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101–118. https://doi.org/10.1016/S0304-3800(02)00205-3

Austin M (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, **200**, 1–19. https://doi.org/10.1016/j.ecolmodel.2006.07.005

Bacouillard L, Baux N, Dauvin J-C, Desroy N, Geiger KJ, Gentil F, Thiébaut É (2020) Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel). *Marine Environmental Research*, **161**, 105062. https://doi.org/10.1016/j.marenvres.2020.105062

Baffreau A, Pezy J-P, Dancie C, Chouquet B, Hacquebart P, Poisson E, Foveau A, Joncourt Y, Duhamel S, Navon M, Marmin S, Dauvin J-C (2017) Mapping benthic communities: An indispensable tool for the preservation and management of the eco-socio-system in the Bay of Seine. *Regional Studies in Marine Science*, **9**, 162–173. https://doi.org/10.1016/j.rsma.2016.12.005

Baltar F, Bayer B, Bednarsek N, Deppeler S, Escribano R, Gonzalez CE, Hansman RL, Mishra RK, Moran MA, Repeta DJ, Robinson C, Sintes E, Tamburini C, Valentin LE, Herndl GJ (2019) Towards Integrating Evolution, Metabolism, and Climate Change Studies of Marine Ecosystems. *Trends in Ecology & Evolution*, **34**, 1022–1033. https://doi.org/10.1016/j.tree.2019.07.003

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *BioScience*, **51**, 633. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries*, **7**, 460–468. https://doi.org/10.2307/1351627

Bouma H, Duiker JMC, de Vries PP, Herman PMJ, Wolff WJ (2001) Spatial pattern of early recruitment of Macoma balthica (L.) and Cerastoderma edule (L.) in relation to sediment dynamics on a highly dynamic intertidal sand¯at. *Journal of Sea Research*, 15. https://doi.org/10.1016/s1385-1101(01)00054-5

Boyden CR, Russell PJC (1972) The Distribution and Habitat Range of the Brackish Water Cockle (Cardium (Cerastoderma) glaucum) in the British Isles. *The Journal of Animal Ecology*, **41**, 719. https://doi.org/10.2307/3205

Brown JH, Stevens GC, Kaufman DM (1996) The Geographic Range: Size, Shape, Boundaries, and Internal Structure. *Annual Review of Ecology and Systematics*, **27**, 597–623. https://doi.org/10.2307/2097247

Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420. https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2

Cade BS, Noon BR, Flather CH (2005) Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology*, **86**, 786–800. https://doi.org/10.1890/04-0785

Cade BS, Terrell JW, Schroeder RL (1999) Estimating effects of limiting factors with regression quantiles. *Ecological Society of America*, **80**, 13. https://doi.org/10.1890/0012-9658(1999)080[0311:eeolfw]2.0.co;2

Carss DN, Brito AC, Chainho P, Ciutat A, de Montaudouin X, Fernández Otero RM, Filgueira MI, Garbutt A, Goedknegt MA, Lynch SA, Mahony KE, Maire O, Malham SK, Orvain F, van der Schatte Olivier A, Jones L (2020) Ecosystem services provided by a non-cultured shellfish species: The common cockle Cerastoderma edule. *Marine Environmental Research*, **158**, 104931. https://doi.org/10.1016/j.marenvres.2020.104931

Chapman M, Tolhurst T, Murphy R, Underwood A (2010) Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. *Marine Ecology Progress Series*, **398**, 33–47. https://doi.org/10.3354/meps08328

Cozzoli F, Bouma T, Ysebaert T, Herman aPMJ (2013) Application of non-linear quantile regression to macrozoobenthic species distribution modelling: comparing two contrasting basins. *Marine Ecology Progress Series*, **475**, 119–133. https://doi.org/10.3354/meps10112

Cozzoli F, Eelkema M, Bouma TJ, Ysebaert T, Escaravage V, Herman PMJ (2014) A Mixed Modeling Approach to Predict the Effect of Environmental Modification on Species Distributions. *PLoS ONE*, **9**, e89131. https://doi.org/10.1371/journal.pone.0089131

Cozzoli F, Smolders S, Eelkema M, Ysebaert T, Escaravage V, Temmerman S, Meire P, Herman PMJ, Bouma TJ (2017) A modeling approach to assess coastal management effects on benthic habitat quality: A case study on coastal defense and navigability. *Estuarine, Coastal and Shelf Science*, **184**, 67–82. https://doi.org/10.1016/j.ecss.2016.10.043

Crossland CJ, Baird D, Ducrotoy J-P, Lindeboom H, Buddemeier RW, Dennison WC, Maxwell BA, Smith SV, Swaney DP (2005) The Coastal Zone — a Domain of Global Interactions. In: *Coastal Fluxes in the Anthropocene* Global Change — The IGBP Series. (eds Crossland CJ, Kremer HH, Lindeboom HJ, Marshall Crossland JI, Le Tissier MDA), pp. 1–37. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/3-540-27851-6_1

Dauvin J-C (2015) History of benthic research in the English Channel: From general patterns of communities to habitat mosaic description. *Journal of Sea Research*, **100**, 32–45. https://doi.org/10.1016/j.seares.2014.11.005

Dauvin JC, Ruellet T, Desroy N, Janson A-L (2006) *Indicateurs benthiques de l'état des peuplements benthiques de l'estuaire marin et moyen et de la partie orientale de la Baie de Seine. Rapport scientifique Seine-Aval 3. Theme 3 : Tableau de bord et indicateurs opérationnels.* GIP Seine Aval.

De Montaudouin X, Bachelet G, Sauriau P-G (2003) Secondary settlement of cockles Cerastoderma edule as a function of current velocity and substratum: a flume study with benthic juveniles. In: *Migrations and Dispersal of Marine Organisms* (eds Jones MB, Ingólfsson A, Ólafsson E, Helgason GV, Gunnarsson K, Svavarsson J), pp. 103–116. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-2276-6_12

Degraer S, Verfaillie E, Willems W, Adriaens E, Vincx M, Van Lancker V (2008) Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. *Continental Shelf Research*, **28**, 369–379. https://doi.org/10.1016/j.csr.2007.09.001

Domínguez R, Vázquez E, Woodin SA, Wethey DS, Peteiro LG, Macho G, Olabarria C (2020) Sublethal responses of four commercially important bivalves to low salinity. *Ecological Indicators*, **111**, 106031. https://doi.org/10.1016/j.ecolind.2019.106031

Donadi S, Westra J, Weerman EJ, van der Heide T, van der Zee EM, van de Koppel J, Olff H, Piersma T, van der Veer HW, Eriksson BK (2013) Non-trophic Interactions Control Benthic Producers on Intertidal Flats. *Ecosystems*, **16**, 1325–1335. https://doi.org/10.1007/s10021-013-9686-8

Donadi S, van der Zee EM, van der Heide T, Weerman EJ, Piersma T, van de Koppel J, Olff H, Bartelds M, van Gerwen I, Eriksson BK (2014) The bivalve loop: Intra-specific facilitation in burrowing cockles through habitat modification. *Journal of Experimental Marine Biology and Ecology*, **461**, 44–52. https://doi.org/10.1016/j.jembe.2014.07.019

Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Eriksson BK, Westra J, van Gerwen I, Weerman E, van der Zee E, van der Heide T, van de Koppel J, Olff H, Piersma T, Donadi S (2017) Facilitation by ecosystem engineers enhances nutrient effects in an intertidal system. *Ecosphere*, **8**, e02051. https://doi.org/10.1002/ecs2.2051

Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends in Ecology & Evolution*, **17**, 177–183. https://doi.org/10.1016/S0169-5347(02)02496-5

Folmer E, Dekinga A, Holthuijsen S (2017) *Species Distribution Models of Intertidal Benthos - Tools for Assessing the Impact of Physical and Morphological Drivers on Benthos and Birds in the Wadden Sea*. NIOZ Royal Netherlands Institute for Sea Research, Texel.

Franklin J (2010) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511810602

Frans VF, Augé AA, Fyfe J, Zhang Y, McNally N, Edelhoff H, Balkenhol N, Engler JO (2022) Integrated SDM database: Enhancing the relevance and utility of species distribution models in conservation management. *Methods in Ecology and Evolution*, **13**, 243–261. https://doi.org/10.1111/2041-210X.13736

Goberville E (2025) Quantile regression as a lens to reveal optimal ecological niches in estuarine ecosystems. *Peer Community in Ecology*, **1**, 100678. https://doi.org/10.24072/pci.ecology.100678

Goberville E, Beaugrand G, Sautour B, Tréguer P, Somlit T (2010) Climate-driven changes in coastal marine systems of western Europe. *Marine Ecology Progress Series*, **408**, 129–147. https://doi.org/10.3354/meps08564

Gosling EM (2003) *Bivalve molluscs: biology, ecology, and culture*. Blackwell Publishing, Oxford ; Malden, MA.

Grassle FJ (2013) Marine Ecosystems. In: *Encyclopedia of Biodiversity* , pp. 45–55. Elsevier. https://doi.org/10.1016/B978-0-12-384719-5.00290-2

Grasso F, Bismuth E, Verney R (2019) CurviSeine Hindcast. https://doi.org/10.12770/8f5ec053-52c8-4120-b031-4e4b6168ff29

Grasso F, Bismuth E, Verney R (2021) Unraveling the impacts of meteorological and anthropogenic changes on sediment fluxes along an estuary-sea continuum. *Scientific Reports*, **11**, 20230. https://doi.org/10.1038/s41598-021-99502-7

Grasso F, Le Hir P (2019) Influence of morphological changes on suspended sediment dynamics in a macrotidal estuary: diachronic analysis in the Seine Estuary (France) from 1960 to 2010. *Ocean Dynamics*, **69**, 83–100. https://doi.org/10.1007/s10236-018-1233-x

Grasso F, Verney R, Le Hir P, Thouvenin B, Schulz E, Kervella Y, Khojasteh Pour Fard I, Lemoine J-P, Dumas F, Garnier V (2018) Suspended Sediment Dynamics in the Macrotidal Seine Estuary (France): 1. Numerical Modeling of Turbidity Maximum Dynamics. *Journal of Geophysical Research: Oceans*, **123**, 558–577. https://doi.org/10.1002/2017JC013185

Guarini J, Blanchard G, Bacher C, Gros P, Riera P, Richard P, Gouleau D, Galois R, Prou J, Sauriau P (1998) Dynamics of spatial patterns of microphytobenthic biomass:inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oléron Bay (France). *Marine Ecology Progress Series*, **166**, 131–141. https://doi.org/10.3354/meps166131

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hale R, Calosi P, McNeill L, Mieszkowska N, Widdicombe S (2011) Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos*, **120**, 661–674. https://doi.org/10.1111/j.1600-0706.2010.19469.x

Hayward PJ, Ryland JS (1995) *Handbook of the marine fauna of north-west Europe*. Oxford University Press.

He KS, Bradley BA, Cord AF, Rocchini D, Tuanmu M-N, Schmidtlein S, Turner W, Wegmann M, Pettorelli N (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, **1**, 4–18. https://doi.org/10.1002/rse2.7

Healy T, Wang Y, Healy J-A (2002) *Muddy Coasts of the World: Processes, Deposits and Function*. Elsevier.

Herman PMJ, Middelburg JJ, Heip CHR (2001) Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. *Continental Shelf Research*, **21**, 2055–2071. https://doi.org/10.1016/S0278-4343(01)00042-5

Herman PMJ, Middelburg JJ, Van De Koppel J, Heip CHR (1999) Ecology of Estuarine Macrobenthos. In: *Advances in Ecological Research* Estuaries. (eds Nedwell DB, Raffaelli DG), pp. 195–240. Academic Press. https://doi.org/10.1016/S0065-2504(08)60194-4

Huang Q, Zhang H, Chen J, He M (2017) Quantile Regression Models and Their Applications: A Review. *Journal of Biometrics & Biostatistics*, **08**. https://doi.org/10.4172/2155-6180.1000354

Hughes B, Levey M, Brown JA, Fountain M, Carlisle A, Litvin S, Greene C, Heady WN, Gleason M (2014) *Nursery functions of U.S. west coast estuaries: the state of knowledge for juveniles of focal fish and invertebrate species*. The Nature Conservancy, Arlington, Va.

Huisman J, Olff H, Fresco L f. m. (1993) A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, **4**, 37–46. https://doi.org/10.2307/3235732

Husson F, Josse J, Le S, Mazet J (2024) FactoMineR: Multivariate Exploratory Data Analysis and Data Mining.

Jiménez-Valverde A, Aragón P, Lobo JM (2021) Deconstructing the abundance-suitability relationship in species distribution modelling. *Global Ecology and Biogeography*, **30**, 327–338. https://doi.org/10.1111/geb.13204

Jones CG, Lawton JH, Shachak M (1994) Organisms as Ecosystem Engineers. *Oikos*, **69**, 373–386. https://doi.org/10.2307/3545850

Jonsson PR, Petersen JK, Karlsson Ö, Loo L-O, Nilsson S (2005) Particle Depletion above Experimental Bivalve Beds: In Situ Measurements and Numerical Modeling of Bivalve Filtration in the Boundary Layer. *Limnology and Oceanography*, **50**, 1989–1998. http://www.jstor.org/stable/3597939

Kassambara A, Mundt F (2020) factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Koenker R (2006) Pseudo R for Quant Reg.

Koenker R, Bassett G (1978) Regression Quantiles. *Econometrica*, **46**, 33. https://doi.org/10.2307/1913643

Koenker R, Hallock K (2000) Quantile regression an introduction. *Journal of Economic Perspectives*, 15.

Koenker R, Hallock KF (2001) Quantile Regression. *Journal of Economic Perspectives*, **15**, 143–156. https://doi.org/10.1257/jep.15.4.143

Koenker R, Machado JAF (1999) Goodness of Fit and Related Inference Processes for Quantile Regression. *Journal of the American Statistical Association*, **94**, 1296–1310. https://doi.org/10.1080/01621459.1999.10473882

Koenker R, Stephen P, Pin TN, Blaise M, Achim Z, Philip G, Cleve M, Yousef S (author of, Victor C, Ivan F-V, Brian DR (2024) quantreg: Quantile Regression.

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, **446**, 285–302. https://doi.org/10.3354/meps09506

Łapucki T, Normant M (2008) Physiological responses to salinity changes of the isopod Idotea chelipes from the Baltic brackish waters. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **149**, 299–305. https://doi.org/10.1016/j.cbpa.2008.01.009

Le Guen C, Tecchio S, Dauvin J-C, De Roton G, Lobry J, Lepage M, Morin J, Lassalle G, Raoux A, Niquil N (2019) Assessing the ecological status of an estuarine ecosystem: linking biodiversity and food-web indicators. *Estuarine, Coastal and Shelf Science*, **228**, 106339. https://doi.org/10.1016/j.ecss.2019.106339

Le Hir P, Cayocca F, Waeles B (2011) Dynamics of sand and mud mixtures: A multiprocess-based modelling strategy. *Continental Shelf Research*, **31**, S135–S149. https://doi.org/10.1016/j.csr.2010.12.009

Le Hir M, Hily C (2005) Macrofaunal diversity and habitat structure in intertidal boulder fields. *Biodiversity & Conservation*, **14**, 233–250. https://doi.org/10.1007/s10531-005-5046-0

L'Ebrellec E, Dauvin J-C, Bacq N (2019) *Macrobenthos en estuaire et baie de Seine : mise à jour de la base de données MABES. Rapport d'étude réalisé par le GIP Seine-Aval.* GIP Seine Aval.

Lehuen A, Oulhen R-M, Zhou Z, de Smit J, van Ijzerloo L, Cozzoli F, Bouma T, Orvain F (2024) Multispecies macrozoobenthic seasonal bioturbation effect on sediment erodibility. *Journal of Sea Research*, **201**, 102525. https://doi.org/10.1016/j.seares.2024.102525

Lemasson AJ, Fletcher S, Hall-Spencer JM, Knights AM (2017) Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: A review. *Journal of Experimental Marine Biology and Ecology*, **492**, 49–62. https://doi.org/10.1016/j.jembe.2017.01.019

Lesourd S, Lesueur P, Brun-Cottan JC, Garnaud S, Poupinet N (2003) Seasonal variations in the characteristics of superficial sediments in a macrotidal estuary (the Seine inlet, France). *Estuarine, Coastal and Shelf Science*, **58**, 3–16. https://doi.org/10.1016/S0272-7714(02)00340-2

Lesourd S, Lesueur P, Fisson C, Dauvin J-C (2016) Sediment evolution in the mouth of the Seine estuary (France): A long-term monitoring during the last 150years. *Comptes Rendus Geoscience*, **348**, 442–450. https://doi.org/10.1016/j.crte.2015.08.001

Li B, Cozzoli F, Soissons LM, Bouma TJ, Chen L (2017) Effects of bioturbation on the erodibility of cohesive versus non-cohesive sediments along a current-velocity gradient: A case study on cockles. *Journal of Experimental Marine Biology and Ecology*, **496**, 84–90. https://doi.org/10.1016/j.jembe.2017.08.002

Madeira D, Fernandes JF, Jerónimo D, Martins P, Ricardo F, Santos A, Domingues MR, Diniz MS, Calado R (2021) Salinity shapes the stress responses and energy reserves of marine polychaetes exposed to warming: From molecular to functional phenotypes. *Science of The Total Environment*, **795**, 148634. https://doi.org/10.1016/j.scitotenv.2021.148634

Mahony KE, Egerton S, Lynch SA, Blanchet H, Goedknegt MA, Groves E, Savoye N, de Montaudouin X, Malham SK, Culloty SC (2022) Drivers of growth in a keystone fished species along the European Atlantic coast: The common cockle Cerastoderma edule. *Journal of Sea Research*, **179**, 102148. https://doi.org/10.1016/j.seares.2021.102148

Malham SK, Hutchinson TH, Longshaw M (2012) A review of the biology of European cockles (Cerastoderma spp.). *Journal of the Marine Biological Association of the United Kingdom*, **92**, 1563–1577. https://doi.org/10.1017/S0025315412000355

Matos FL, Vaz N, Picado A, Dias JM, Maia F, Gaspar MB, Magalhães L (2023) Assessment of Habitat Suitability for Common Cockles in the Ria the Aveiro Lagoon Under Average and Projected Environmental Conditions. *Estuaries and Coasts*, **46**, 512–525. https://doi.org/10.1007/s12237-022-01136-z

Medeiros IPM, Faria SC, Souza MM (2020) Osmoionic homeostasis in bivalve mollusks from different osmotic niches: Physiological patterns and evolutionary perspectives. *Comparative*

Biochemistry and Physiology Part A: Molecular & Integrative Physiology, **240**, 110582. https://doi.org/10.1016/j.cbpa.2019.110582

Melo-Merino SM, Reyes-Bonilla H, Lira-Noriega A (2020) Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. *Ecological Modelling*, **415**, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837

Mengual B, Le Hir P, Rivier A, Caillaud M, Grasso F (2020) Numerical modeling of bedload and suspended load contributions to morphological evolution of the Seine Estuary (France). *International Journal of Sediment Research*, **36**, 723–735. https://doi.org/10.1016/j.ijsrc.2020.07.003

Morelle J, Claquin P, Orvain F (2020) Evidence for better microphytobenthos dynamics in mixed sand/mud zones than in pure sand or mud intertidal flats (Seine estuary, Normandy, France). *PLOS ONE*, **15**, e0237211. https://doi.org/10.1371/journal.pone.0237211

Morelle J, Schapira M, Orvain F, Riou P, Lopez PJ, Duplessix O, Rabiller E, Maheux F, Simon B, Claquin P (2018) Annual Phytoplankton Primary Production Estimation in a Temperate Estuary by Coupling PAM and Carbon Incorporation Methods. *Estuaries and Coasts*, **41**, 1337–1355. https://doi.org/10.1007/s12237-018-0369-8

Murray NJ, Phinn SR, DeWitt M, Ferrari R, Johnston R, Lyons MB, Clinton N, Thau D, Fuller RA (2019) The global distribution and trajectory of tidal flats. *Nature*, **565**, 222–225. https://doi.org/10.1038/s41586-018-0805-8

Ong EZ, Briffa M, Moens T, Van Colen C (2017) Physiological responses to ocean acidification and warming synergistically reduce condition of the common cockle Cerastoderma edule. *Marine Environmental Research*, **130**, 38–47. https://doi.org/10.1016/j.marenvres.2017.07.001

Orvain F, Lefebvre S, Montepini J, Sébire M, Gangnery A, Sylvand B (2012) Spatial and temporal interaction between sediment and microphytobenthos in a temperate estuarine macro-intertidal bay. *Marine Ecology Progress Series*, **458**, 53–68. https://doi.org/10.3354/meps09698

Peteiro LG, Woodin SA, Wethey DS, Costas-Costas D, Martínez-Casal A, Olabarria C, Vázquez E (2018) Responses to salinity stress in bivalves: Evidence of ontogenetic changes in energetic physiology on Cerastoderma edule. *Scientific Reports*, **8**, 8329. https://doi.org/10.1038/s41598-018-26706-9

Rakotomalala C, Grangeré K, Ubertini M, Forêt M, Orvain F (2015) Modelling the effect of Cerastoderma edule bioturbation on microphytobenthos resuspension towards the planktonic food web of estuarine ecosystem. *Ecological Modelling*, **316**, 155–167. https://doi.org/10.1016/j.ecolmodel.2015.08.010

Richards D, Lavorel S (2023) Niche theory improves understanding of associations between ecosystem services. *One Earth*, **6**, 811–823. https://doi.org/10.1016/j.oneear.2023.05.025

Richardson CA, Crisp DJ, Runham NW (1980) Factors influencing shell growth in *Cerastoderma edule*. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **210**, 513–531. https://doi.org/10.1098/rspb.1980.0150

Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, Possingham HP, Richardson AJ (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, **20**, 789–802. https://doi.org/10.1111/j.1466-8238.2010.00636.x

Robinson NM, Nelson WA, Costello MJ, Sutherland JE, Lundquist CJ (2017) A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice. *Frontiers in Marine Science*, **4**. https://doi.org/10.3389/fmars.2017.00421

Roland A, Ardhuin F (2014) On the developments of spectral wave models: numerics and parameterizations for the coastal ocean. *Ocean Dynamics*, **64**, 833–846. https://doi.org/10.1007/s10236-014-0711-z

Saint-Béat B, Dupuy C, Bocher P, Chalumeau J, De Crignis M, Fontaine C, Guizien K, Lavaud J, Lefebvre S, Montanié H, Mouget J-L, Orvain F, Pascal P-Y, Quaintenne G, Radenac G, Richard P, Robin F, Vézina AF, Niquil N (2013) Key Features of Intertidal Food Webs That Support Migratory Shorebirds (B Fenton, Ed,). *PLoS ONE*, **8**, e76739. https://doi.org/10.1371/journal.pone.0076739

Santos C, Cabral S, Carvalho F, Sousa A, Goulding T, Ramajal J, Medeiros JP, Silva G, Angélico MM, Gaspar MB, Brito AC, Costa JL, Chainho P (2022) Spatial and Temporal Variations of Cockle (Cerastoderma spp.) Populations in Two Portuguese Estuarine Systems With Low Directed Fishing Pressure. *Frontiers in Marine Science*, **9**. https://doi.org/10.3389/fmars.2022.699622

Sauriau P-G, Kang C-K (2000) Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder Cerastoderma edule (Mollusca, Bivalvia) in the Marennes-Oléron Bay. In: *Island, Ocean and Deep-Sea Biology* Developments in Hydrobiology. (eds Jones MB, Azevedo JMN, Neto AI, Costa AC, Martins AMF), pp. 317–329. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-1982-7_29

Schickele A, Leroy B, Beaugrand G, Goberville E, Hattab T, Francour P, Raybaud V (2020) Modelling European small pelagic fish distribution: Methodological insights. *Ecological Modelling*, **416**, 108902. https://doi.org/10.1016/j.ecolmodel.2019.108902

Schröder HK, Andersen HE, Kiehl K (2005) Rejecting the mean: Estimating the response of fen plant species to environmental factors by non-linear quantile regression. *Journal of Vegetation Science*, **16**, 373–382. https://doi.org/10.1111/j.1654-1103.2005.tb02376.x

Schulz E, Grasso F, Le Hir P, Verney R, Thouvenin B (2018) Suspended Sediment Dynamics in the Macrotidal Seine Estuary (France): 2. Numerical Modeling of Sediment Fluxes and Budgets Under Typical Hydrological and Meteorological Conditions. *Journal of Geophysical Research: Oceans*, **123**, 578–600. https://doi.org/10.1002/2016JC012638

Shi B, Pratolongo PD, Du Y, Li J, Yang SL, Wu J, Xu K, Wang YP (2020) Influence of Macrobenthos (Meretrix meretrix Linnaeus) on Erosion-Accretion Processes in Intertidal Flats: A Case Study From a Cultivation Zone. *Journal of Geophysical Research: Biogeosciences*, **125**, e2019JG005345. https://doi.org/10.1029/2019JG005345

Singer A, Millat G, Staneva J, Kröncke I (2017) Modelling benthic macrofauna and seagrass distribution patterns in a North Sea tidal basin in response to 2050 climatic and environmental scenarios. *Estuarine, Coastal and Shelf Science*, **188**, 99–108. https://doi.org/10.1016/j.ecss.2017.02.003

Soissons LM, Gomes da Conceiçâo T, Bastiaan J, van Dalen J, Ysebaert T, Herman PMJ, Cozzoli F, Bouma TJ (2019) Sandification vs. muddification of tidal flats by benthic organisms: A flume study. *Estuarine, Coastal and Shelf Science*, **228**, 106355. https://doi.org/10.1016/j.ecss.2019.106355

Srivastava V, Lafond V, Griess VC (2019) Species distribution models (SDM): applications, benefits and challenges in invasive species management. *CABI Reviews*, **2019**, 1–13. https://doi.org/10.1079/PAVSNNR201914020

Stephenson F, Gladstone-Gallagher RV, Bulmer RH, Thrush SF, Hewitt JE (2022) Inclusion of biotic variables improves predictions of environmental niche models. *Diversity and Distributions*, **28**, 1373–1390. https://doi.org/10.1111/ddi.13546

Tecchio S, Chaalali A, Raoux A, Tous Rius A, Lequesne J, Girardin V, Lassalle G, Cachera M, Riou P, Lobry J, Dauvin J-C, Niquil N (2016) Evaluating ecosystem-level anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary. *Ecological Indicators*, **61**, 833–845. https://doi.org/10.1016/j.ecolind.2015.10.036

Thomas Y, Bacher C (2018) Assessing the sensitivity of bivalve populations to global warming using an individual-based modelling approach. *Global Change Biology*, **24**, 4581–4597. https://doi.org/10.1111/gcb.14402

Thrush S, Hewitt J, Herman P, Ysebaert T (2005) Multi-scale analysis of species-environment relationships. *Marine Ecology-Progress Series*, **302**, 13–26. https://doi.org/10.3354/Meps302013

Thrush S, Hewitt J, Norkko A, Nicholls P, Funnell G, Ellis J (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Marine Ecology Progress Series*, **263**, 101–112. https://doi.org/10.3354/meps263101

Ubertini M, Lefebvre S, Gangnery A, Grangeré K, Le Gendre R, Orvain F (2012) Spatial Variability of Benthic-Pelagic Coupling in an Estuary Ecosystem: Consequences for Microphytobenthos

Resuspension Phenomenon (S Thrush, Ed.,). *PLoS ONE*, **7**, e44155. https://doi.org/10.1371/journal.pone.0044155

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212–224. https://doi.org/10.1007/BF00327905

Van Colen C, Montserrat F, Vincx M, Herman PMJ, Ysebaert T, Degraer S (2010) Macrobenthos recruitment success in a tidal flat: Feeding trait dependent effects of disturbance history. *Journal of Experimental Marine Biology and Ecology*, **385**, 79–84. https://doi.org/10.1016/j.jembe.2010.01.009

Van Der Wal D, Herman P, Forster R, Ysebaert T, Rossi F, Knaeps E, Plancke Y, Ides S (2008) Distribution and dynamics of intertidal macrobenthos predicted from remote sensing: response to microphytobenthos and environment. *Marine Ecology Progress Series*, **367**, 57–72. https://doi.org/10.3354/meps07535

Van Der Wal D, Wielemaker-van Den Dool A, Herman PMJ (2010) Spatial Synchrony in Intertidal Benthic Algal Biomass in Temperate Coastal and Estuarine Ecosystems. *Ecosystems*, **13**, 338–351. https://doi.org/10.1007/s10021-010-9322-9

Van Der Wal D, Ysebaert T, Herman PMJ (2017) Response of intertidal benthic macrofauna to migrating megaripples and hydrodynamics. *Marine Ecology Progress Series*, **585**, 17–30. https://doi.org/10.3354/meps12374

Vera M, Wilmes SB, Maroso F, Hermida M, Blanco A, Casanova A, Iglesias D, Cao A, Culloty SC, Mahony K, Orvain F, Bouza C, Robins PE, Malham SK, Lynch S, Villalba A, Martínez P (2023) Heterogeneous microgeographic genetic structure of the common cockle (Cerastoderma edule) in the Northeast Atlantic Ocean: biogeographic barriers and environmental factors. *Heredity*, **131**, 292–305. https://doi.org/10.1038/s41437-023-00646-1

Verdelhos T, Veríssimo H, Marques JC, Anastácio P (2021) Behavioural Responses of Cerastoderma edule as Indicators of Potential Survival Strategies in the Face of Flooding Events. *Applied Sciences*, **11**, 6436. https://doi.org/10.3390/app11146436

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342. https://doi.org/10.1890/10-1171.1

Wiesebron L, Teeuw L, van Dalen J, van Ijzerloo L, Troost K, Walles B, Ysebaert T, Bouma T (2022) Contrasting strategies to cope with storm-induced erosion events: a flume study comparing a native vs. introduced bivalve. *Limnology and Oceanography*, **67**, 2572–2585. https://doi.org/10.1002/lno.12223

Ysebaert T, Herman PMJ (2002) Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. *Marine Ecology Progress Series*, **244**, 105–124. https://doi.org/10.3354/meps244105

Ysebaert T, Meire P, Herman PMJ, Verbeek H (2002) Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series*, **225**, 79–95. https://doi.org/10.3354/meps225079

Zhou Z, Bouma TJ, Fivash GS, Ysebaert T, van IJzerloo L, van Dalen J, van Dam B, Walles B (2022) Thermal stress affects bioturbators' burrowing behavior: A mesocosm experiment on common cockles (Cerastoderma edule). *Science of The Total Environment*, **824**, 153621. https://doi.org/10.1016/j.scitotenv.2022.153621