Estuaries and Coasts
https://doi.org/10.1007/s12237-022-01136-z

Assessment of Habitat Suitability for Common Cockles in the Ria the Aveiro Lagoon Under Average and Projected Environmental Conditions

Fábio L. Matos[1] · Nuno Vaz[2] · Ana Picado[2] · João M. Dias[2] · Francisco Maia[3] · Miguel B. Gaspar[4,5] · Luísa Magalhães[1]

Received: 11 May 2022 / Revised: 11 October 2022 / Accepted: 11 October 2022

Abstract
The common cockle *Cerastoderma edule* is a widespread bivalve species inhabiting estuarine systems across the North East Atlantic, where it provides several ecosystem services, and represents a valuable fishery resource for local economies. However, anthropogenic pressure and more frequent extreme weather events threaten the resilience of the species. Spatially explicit information on species distribution is critical for the implementation of management and conservation practices. This study assessed the potential distribution of *C. edule* in the Ria de Aveiro by estimating the habitat suitability using an ensemble approach based on ecological niche modeling and recently developed hydrodynamic and water quality models to forecast both average and projected estuarine conditions. The models were developed for the summer of 2013 and spring of 2019 and potential range shifts in the species distribution were forecasted under projected environmental conditions: high and low estimates of freshwater discharge, a 2 °C increase in water temperature, and the combined effect of low freshwater discharge and increased water temperature. The results suggest that salinity, time of submersion, and current velocity play an important role in the distribution of cockles, and large areas were consistently classified with high habitat suitability. Increased freshwater discharge (both seasons) and low discharge coupled to increased temperature (spring) resulted in large decreases in suitable habitat. Conversely, low freshwater discharges and average (unchanged) temperatures increased the suitable habitat in the outermost regions of the Ria. The spatially explicit information provided contributes to a better understanding of the vulnerability of *C. edule* in the Ria de Aveiro to extreme weather events (e.g., droughts, river floods) and may support adaptive management strategies of the cockle fishery during these conditions. Moreover, this approach can be transferred to other estuarine ecosystems for which data describing the environmental conditions (e.g., derived from numerical models), and information about species presence are available (including data-poor species).

Keywords *Cerastoderma edule* · Climate change · Ensemble model · Potential distribution

Introduction

The common cockle *Cerastoderma edule* is a suspension-feeding bivalve that inhabits transitional soft-sediment areas of the eastern Atlantic from Norway to Senegal (Hayward and Ryland 1995; Tebble 1966). Cockles provide multiple ecosystem services, including supporting and provisional services (Carss et al. 2020). For instance, through bioturbation, *C. edule* incorporates fine suspended particles into the sediment matrix, affecting its properties (Cozzoli et al. 2020; Dairain et al. 2020; Soissons et al. 2019)

Communicated by Mark J. Brush

✉ Fábio L. Matos
fmatos@ua.pt

[1] Department of Biology & CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

[2] Department of Physics & CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

[3] Portuguese Institute for the Sea and Atmosphere (IPMA), Avenida Doutor David Cristo s/n, 3800-366 Aveiro, Portugal

[4] Centro de Olhão, Portuguese Institute for the Sea and Atmosphere (IPMA), Av. 5 de Outubro s/n, 8700-335 Olhão, Portugal

[5] Centre of Marine Sciences (CCMAR), University of Algarve, Campus Universitário de Gambelas, 8005-139 Faro, Portugal

and influencing biogeochemical cycles (Rakotomalala et al. 2015). Moreover, cockles are able to improve water quality through filtration, by decreasing water turbidity and removing excess nutrients (e.g., nitrate, phosphorus) (Van der Schatte Olivier et al. 2018). In addition to the inherent ecological value of *C. edule* as an ecosystem engineer and major prey for several organisms (Carss et al. 2020), the common cockle is among the most targeted bivalve species in coastal systems across Europe (Mahony et al. 2020).

Increasing the current knowledge on the distribution of marine living resources and their behavioral responses to the environment is of utmost importance for the development of effective management plans and future conservation actions. The distribution of bivalves in intertidal areas is influenced by several environmental factors including salinity (Peteiro et al. 2018; Verdelhos et al. 2015a), water temperature (Callaway et al. 2013; Singer et al. 2017), current velocity (Kater et al. 2006; Rullens et al. 2021), and emersion time (Ramón 2003). Variations in these parameters subject individuals to physiological stress and may affect the food supply and larval recruitment (Kater et al. 2006; De Montaudouin and Bachelet 1996). Pronounced seasonal cycles in the physiology of *C. edule*, related to endogenous and environmental factors (e.g., temperature) are also recognized, including respiration rate and feeding activity (Iglesias and Navarro 1991; Newell and Bayne 1980). Biotic interactions (e.g., predation, parasitism) and anthropogenic activities (e.g., fisheries) may also determine the distribution of cockles (Mahony et al. 2022). The interplay of these variables may lead to yearly fluctuations in bivalve productivity that combined with increasing anthropogenic pressure and climate change (e.g., sea level rise, higher frequencies of extreme weather events such as heat waves, droughts, and heavy precipitation (IPCC 2014)) subject species to increasing physiological stress and raise concerns about the sustainable exploitation of this resource in the mid-term.

The design of management plans frequently depends on spatially explicit data, including information on the species distribution. Ecological niche modeling (ENM) frameworks have been widely used as indirect methods to estimate the species potential distribution and habitat suitability by using presence data coupled with spatial environmental information (Peterson et al. 2015), including for marine species (Kater et al. 2006; Melo-Merino et al. 2020). The outputs of ENM include the projection of the species-environment-relationship on the geographic space producing maps which can assist managers and decision-makers in the development of management and conservation plans (Guisan et al. 2013). The applications of ENM go beyond determining climate–range relationships to characterize species' tolerance limits to present environmental conditions and have been also used to project species response to different climatic scenarios (Araújo et al. 2005). The transferability of correlative ENM predictions to different spatiotemporal conditions is not straightforward and faces challenges derived from data limitations of projecting models to distinct conditions from the ones used for fitting, and from the complexity and plasticity inherent to biological systems (Sequeira et al. 2018; Urban et al. 2016; Yates et al. 2018). Nevertheless, transferability of ENM predictions may have particular relevance for the development of conservation and management measures for marine ecosystems (e.g., Lauria et al. 2015).

The use of ENM in the marine environment has benefited from advances in remote sensing and numerical modeling approaches, capable of efficiently describing the physical conditions of a highly dynamic environment (e.g., Vargas et al. 2017; Vaz et al. 2019). These advances have proven critical for the development of more realistic ENM's with a greater chance of having a significant impact on the development of effective living resources management measures (Cozzoli et al. 2014; Reiss et al. 2014; Tommasi et al. 2017).

Common cockles are widespread and generally abundant in the Ria de Aveiro, a shallow coastal lagoon located on the North coast of Portugal (Maia et al. 2021). In Portugal, this species represented 60% of the total reported bivalve catch in 2020 (INE 2020) and in Ria de Aveiro, the exploitation of *C. edule* provides a major source of income for many households, contributing significantly to the regional economy (Braga et al. 2022; Maia et al. 2021). The lack of a specific and effective management plan for cockle fisheries in Portugal (Maia et al. 2021) hampers both sustainable fisheries and conservation efforts, particularly under climate change. The information on the species distribution is still fragmented and the management of the cockle fishery frequently relies on population criteria (e.g., minimum capture sizes) (Maia et al. 2021). In the context presented above, this study was designed to gain insights into the current distribution of *C. edule* in the Ria de Aveiro by estimating the habitat suitability and predicting range shifts expected under several scenarios of weather conditions including both increases and decreases in rainfall and increased seawater temperature. These results provide scientific-based evidence to assist resource managers to regulate and better plan the species harvest in the study area by: (i) supporting the design of special areas of conservation and management interest, (ii) enabling the development of adaptive management strategies, and (iii) providing information about the degree of uncertainty of model predictions.

Material and Methods

Study Area

The Ria de Aveiro was chosen as a case study due to the widespread distribution and abundance of *C. edule* in this coastal lagoon, and to the ecological importance and socio-economic relevance of the species in Portugal. This decision was also supported by the availability of a robust dataset on the species presence within the study area and on environmental dynamics in this coastal lagoon.

The Ria de Aveiro is the most extensive coastal lagoon in Portugal. It is located on the NW coast of Portugal and is connected to the Atlantic Ocean by an artificial inlet constructed in 1808 (Dias and Mariano 2011). The lagoon has a maximum width of 8.5 km, a length of 45 km, and an average depth (over the local datum) of ~ 1 m, and has four main channels: the Mira, São Jacinto, Ílhavo, and Espinheiro channels. The hydrodynamics of the Ria de Aveiro are dominated by mixed semidiurnal tides, with a mean tidal range of ~ 2.0 m at the inlet (Dias et al. 1999). The tidal range at the inlet varies from 0.6 m (neap tide) to about 3.2 m (spring tides) (Dias et al. 2000). The strongest currents are observed at the inlet channel, with values higher than 2 ms^{-1} (Vaz et al. 2009). The Ria de Aveiro has five main freshwater tributaries that control the transport of water properties in the lagoon (Dias et al. 1999; Moreira et al. 1993; Vaz et al. 2016). The total mean estimated freshwater input is approximately 1.8×10^6 m^3 during a tidal cycle (Moreira et al. 1993), which is considerably lower than the total tidal prism volume for neap and spring tide conditions, estimated to be 65.8×10^6 m^3 and 139.7×10^6 m^3, respectively (Lopes et al. 2013; Picado et al. 2010). This shallow estuarine system displays intense tidal currents, providing a well-mixed lagoon system regarding water properties (Dias et al. 1999). In fact, the salinity and water temperature gradients are weak across the water column and depend mostly on the input of freshwater. In contrast, the longitudinal gradient of water temperature and salinity varies widely along the main channels of the lagoon (Dias 2001; Vaz et al. 2005).

Due to morphologic changes induced mostly by human action (i.e., dredging operations to facilitate navigation), important changes in lagoon hydrodynamics have taken place over the last few decades, reflecting increased tidal amplitudes and currents, as well as increased salt intrusion, with these changes being amplified towards the head of the main channels (Dias et al. 2021).

Species Presence Data

The presence data (Fig. 1) used in the present study were obtained from biological surveys conducted by the Portuguese Institute of Sea and Atmosphere (IPMA) in the summer of 2013 and spring of 2019 under the scope of two European Interreg projects (GEPETO and COCKLES). A total of 828 stations, spaced 200–400 m apart, were sampled along 290 transects using a hand dredge with a 10 mm mesh net. Each transect typically included three stations, one on each side of the channel in the intertidal zone and one station in the middle of the channel (subtidal zone).

No data treatment aiming to reduce spatial autocorrelation in the presence data was applied. This decision was made considering that (1) the presence records were produced from a systematic and comprehensive sampling approach across the study area, and (2) the resolution of the environmental data (see the "Environmental Data" section) was smaller than the minimum distance between sampling stations. Information on species absence was not considered since the study area is subjected to an intense fishing activity directed towards *C. edule* (e.g., Braga et al. 2022), and therefore, absence data is heavily biased by human influence.

Environmental Data

In this study, a combination of estuarine variables were computed by the numerical model DELFT3D (Deltares 2014) which was implemented and validated for the Ria de Aveiro by Dias et al. (2021). The model provides information for the hydrodynamical setting and water biogeochemical variables in an irregular horizontal grid with a spatial resolution ranging from 50 to 100 m (Table 1). The values of each environmental variable were estimated for the months with biological sampling (i.e., June, July and August of 2013, and April, May and June of 2019) and then averaged to produce a single data layer for each variable and year. These new layers represent the average condition of the summer of 2013 and spring of 2019 and were then used to fit two independent ENM. In addition to the estuarine conditions coincident with the timeframe of the presence data (i.e., summer of 2013 and spring of 2019; hereafter referred as average conditions), the environmental conditions at the Ria de Aveiro for spring and summer were estimated according to four different environmental and hydrological scenarios. Three independent scenarios were built considering low and high freshwater discharge from the main tributaries, and a 2 °C increase in water temperature. Finally, a fourth scenario was built estimating the combined effect of a 2 °C increase in water temperature and low freshwater discharge. The low freshwater discharge scenario is a proxy for low rainfall conditions, and the high river discharge scenario is a proxy for a maximum rainfall scenario. Freshwater discharge of the main tributary river tributaries to the lagoon imposed on the fluvial boundaries of the DELFT3D-FLOW was obtained from the results of the SWIM model (Stefanova et al. 2015), using a period from 1981 to 2010

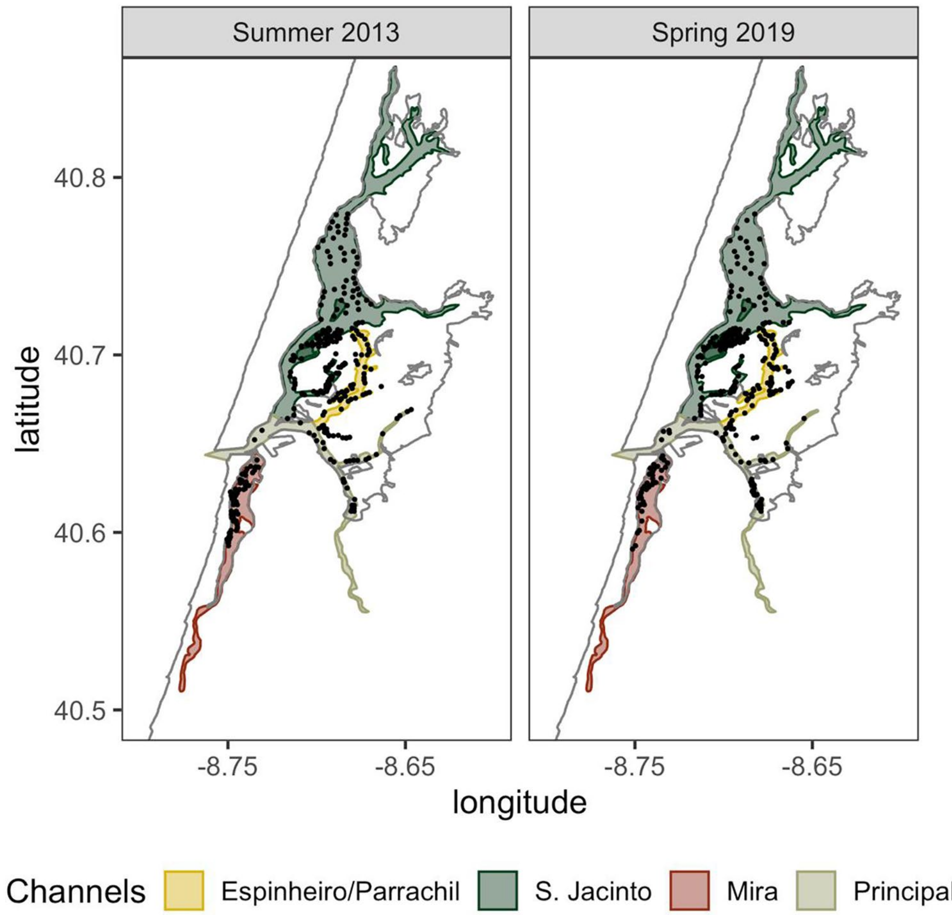

Fig. 1 Spatial distribution of presence records of *Cerastoderma edule* in the Ria de Aveiro in the summer of 2013 and spring of 2019. The major channels of the lagoon are delimited by the colored polygons: yellow — Espinheiro/Parrachil channel, green — S. Jacinto channel, reddish — Mira channel, and pearl — Principal/Ílhavo channel

where maximum and minimum values were extracted. To simulate low freshwater discharge conditions, values from 0.4 up to 5 $m^3\ s^{-1}$ were imposed at the mouth of the rivers; to simulate high discharge conditions, freshwater discharges varied between 11 and 370 $m^3\ s^{-1}$ at the discharge points. The value of 2 °C was selected according to the long-term ensemble projections for the Portuguese coast of the Sixth Coupled Model Intercomparison Project (CMIP6), considering the pessimistic scenario (SSP5-8.5) (Gutiérrez et al. 2021). In the Supplementary Material, a brief description of the estuarine hydrodynamic and water quality models is presented, as well as the implementations used in this study.

Table 1 List of environmental variables describing the environmental condition at the Ria the Aveiro (average values and their range) for the summer of 2013 and spring of 2019

Variables	Units	Average values		Values range	
		2013 Summer	2019 Spring	2013 Summer	2019 Spring
Salinity	-	29.1	25.1	3.3–34.6	0.8–33.9
Water temperature	°C	21.1	17.2	16.4–24.7	14.6–19.9
Chlorophyll-a	mg L^{-1}	0.003	0.005	0.001–0.015	0.002–0.037
Ammonium		0.011	0.038	0.002–0.227	0.011–0.334
Nitrate		0.404	1.882	0.091–3.662	0.464–7.338
Phosphate		0.030	0.072	0.006–0.065	0.038–0.156
Dissolved oxygen		7.275	7.789	2.023–8.191	7.294–8.191
pH	-	8.0	7.6	4.5–8.6	6.9–8.3
Submersion time — spring tide	Hours	10.6	10.8	0.8–12.5	1.8–12.5
Submersion time — neap tide		10.3	10.5	0–12.5	0–12.5
Current velocity	m s^{-1}	0.230	0.301	0.008–1.721	0.009–1.735

The variables included in the ecological niche models (ENM) are highlighted in boldface

Data obtained from the environmental variables computed by the numerical model of the Ria de Aveiro were interpolated to a regular grid (100×100 m) by fitting a universal kriging model based on the 12 nearest values of each focal cell using the automap package for R (Hiemstra et al. 2009). Spatial autocorrelation between environmental variables was statistically assessed using Pearson's correlation coefficient (*r*), and the function remove Collinearity available through the R package virtual species (Leroy et al. 2016). A correlation coefficient between two variables greater than 0.8 dictated the exclusion of one of those variables from the ENM (Supplementary Figure S1).

Estimate of the Habitat Suitability Under Average Conditions

The ENM was developed using the R package sdm (version 1.1–8, Naimi and Araújo 2016). An ensemble modeling approach was adopted for this study (Araújo and New, 2007), combining the output of multiple single-algorithm models into a unique prediction according to their individual performances. Hence, this approach accounts for the variability among model predictions and differences resulting from the use of distinct algorithms to estimate the species ecological niche. The consensus predictions were derived from single models based on three algorithms: boosted regression trees (BRT), random forest (RF), and flexible discriminate analysis (FDA). The BTR algorithm uses the boosting method to combine multiple models that relate the response variable with predictors using recursive binary splits (i.e., regression trees) (Elith et al. 2008). On the other hand, the RF algorithm uses a bootstrap aggregation procedure of multiple classification trees and then averages the output using committee averaging (Hastie et al. 2009). The FDA is a nonparametric version of the discriminate analysis that replaces linear regression with a nonparametric regression technique for multigroup nonlinear classification (Hastie et al. 1994). A dataset of pseudo-absences with the same number of presences was generated for model fitting and evaluation. Pseudo-absences were randomly selected outside of the suitable area estimated by a rectilinear surface envelope from the presences record (surface range envelope, Thuiller et al. 2009).

Model accuracy was evaluated using a fivefold cross-validation procedure, repeated 10 times, resulting in 50 replications per method. Models were fitted for each replication using four random cross-validation splits for training, and the fifth withheld data split was used for evaluation. The ensemble models were obtained based on the weighted average of the single-algorithm estimations retained according to the values of the true skill statistic (TSS) metric. The TSS compares the number of correct predictions minus those assigned by chance in a perfect forecast (Allouche et al. 2006). The selected threshold for TSS was the one that maximized both the sum of PPV (positive predictive value) and NPV (negative predictive value) value of models' estimation.

Variable importance was assessed using a randomization procedure that measures the Pearson's correlation between the standard predictions and the predictions where the variable of interest has been randomly permuted (Naimi and Araújo 2016; Thuiller et al. 2009). A high correlation between the two predictions means that the variable permutated is not important for the model prediction. The model's response curves were estimated by the evaluation strip procedure (Elith et al. 2005) implemented in the sdm package.

The model outputs are a continuous representation of the habitat suitability index (HSI) ranging from 0 to 1, with values close to 1 indicating the most suitable areas. The predictions of the ensemble models for average conditions were evaluated using the Continuous Boyce Index (CBI) (Boyce et al. 2002; Hirzel et al. 2006), calculated using the "ecospat" package which has been described as the most appropriate metric to evaluate presence-only models (Di Cola et al. 2017). The CBI is a threshold independent metric ranging from − 1 to 1: values close to 1 indicate a good agreement between the model predictions and the distribution of presences (i.e., areas with a high number of occurrences are scored with high suitability values), while values close to − 1 indicate that the model performed poorly (Hirzel et al. 2006). Values close to zero means that model estimation is not different from a random prediction.

A map of uncertainty related to the ensemble model prediction was generated based on the variation between estimates of the single algorithm models. The uncertainty values range between 0 and 1, with values close to zero meaning low uncertainty (i.e., high agreement between single algorithm models' estimates), and values close to one referring to the highest level of uncertainty (Naimi and Araújo 2016).

Model Transferability Assessment and Model Projections for Different Environmental Conditions

To assess the potential of transferability of the ensemble models, the model developed for the summer of 2013 was projected into the environmental conditions for 2019 and predictions evaluated using presence data for the extrapolated year (i.e., 2019) and vice versa. Transferability of the ensemble models was evaluated using three measures of accuracy: the area under the curve (AUC), sensitivity (i.e., the percentage of presence correctly predicted), and the CBI. For the AUC and sensitivity metrics (Allouche et al. 2006), the average score was calculated using a cross-validation framework with five independent spatial blocks randomly assigned to separate training and testing datasets (Assis et al. 2022). This approach was implemented using the R packages blockCV (Valavi et al. 2019) and precrec (Saito and Rehmsmeier 2017). The spring and summer models were then projected onto the different scenarios of environmental conditions (i.e., low and high freshwater discharge, a 2 °C increase in water temperature, and the combined effect of a 2 °C increase in water temperature with a low freshwater discharge scenario) to estimate the potential impacts of these environmental conditions on the habitat suitability of the Ria de Aveiro for the presence of *C. edule*.

Results

A total of 150 single-algorithm models for each year were fitted using 286 common cockle presence records in the models of 2013, and 271 for 2019 (Fig. 1) combined with six environmental variables describing the Ria of Aveiro conditions in each year. The ensemble models for the average conditions reached high predictive performance according to the Boyce Index (CBI = 0.935 in 2013 and CBI = 0.937 in 2019).

Environmental Suitability — Average Conditions

Overall, the predictions of the models were similar in both years, with large areas consistently classified with high environmental suitability (HSI ≥ 0.8, hereafter defined as core habitat regions) for the presence of the common cockle in the Ria de Aveiro (Fig. 2). The uncertainty related to the models' predictions showed that the core habitat regions coincide mostly with areas with low uncertainty associated with the models' predictions (Supplementary Figure S2).

Figure 3 shows the model response curves for the summer of 2013 and spring of 2019. Generally, the common cockle found increasingly suitable conditions with the increase of salinity and nitrate concentrations, currents velocity varying

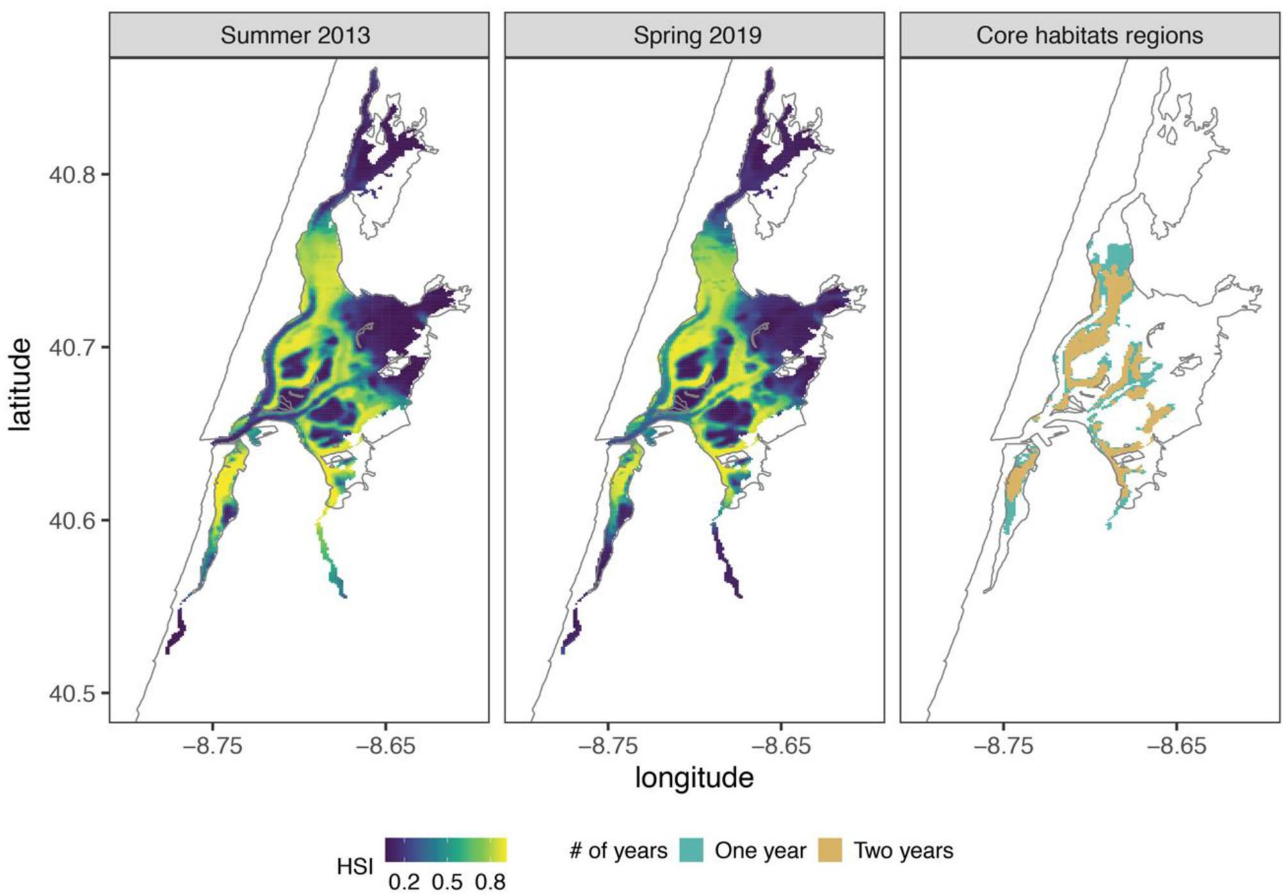

Fig. 2 Estimates of the environmental suitability for the presence of the common cockle in the Ria de Aveiro in the summer of 2013 (left panel) and spring of 2019 (middle panel). Color scale ranging from 0 to 1, with values close to zero representing low habitat suitability, and values close to one high habitat suitability. The core habitat regions (right panel) defined by a habitat suitability index (HSI) ≥ 0.8, are color coded according to the number of years that the model prediction agreed: turquoise — 1 year, brownish — 2 years

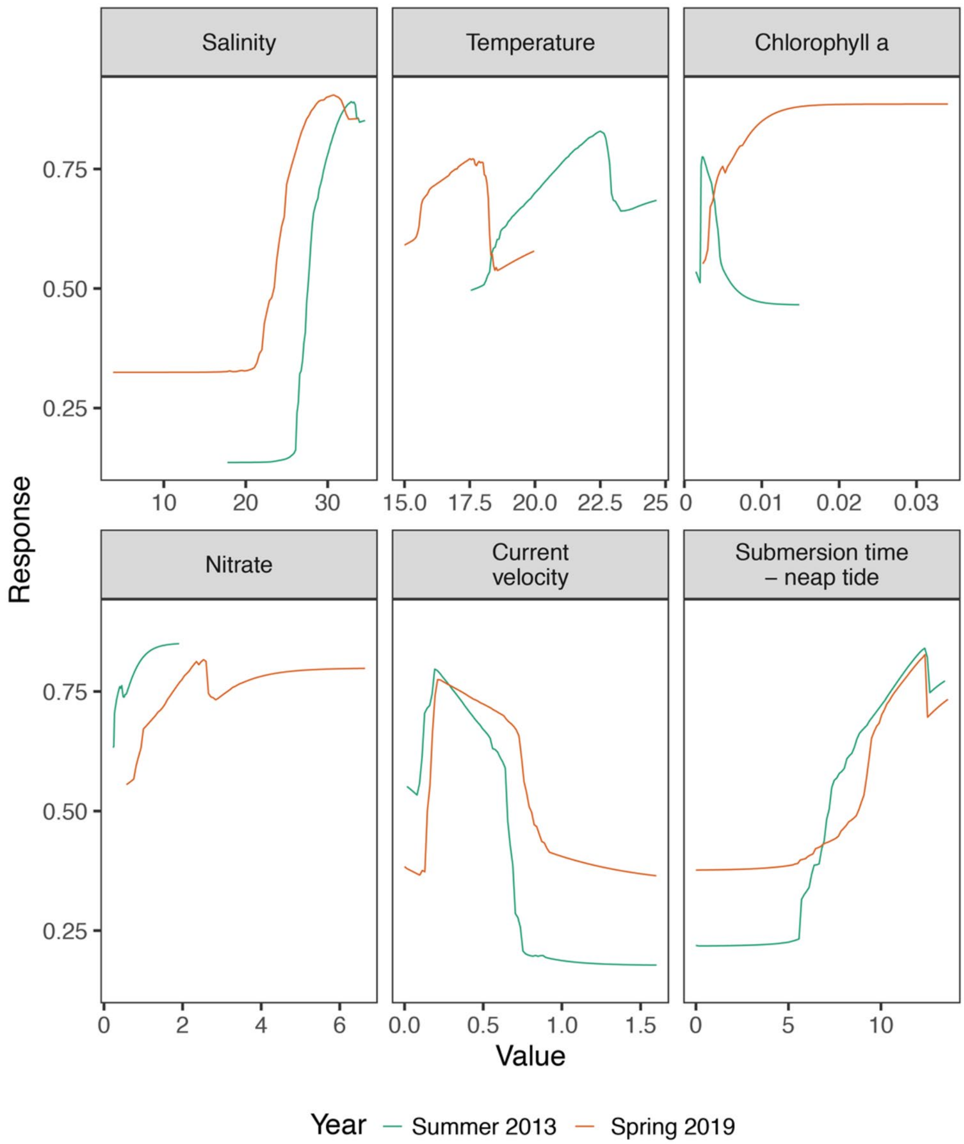

Fig. 3 Response curves for each environmental variable used in the ensemble models developed for the summer of 2013 (turquoise lines) and spring of 2019 (orange lines). Environmental gradients are represented in the x-axis, and the suitability prediction values in the y-axis

around 0.2 and 0.6 m s^{-1}, and when subjected to submersion periods lasting between 11 and 14 h. For the other predictors, changes in the environmental background due to seasonal variability resulted in different model responses. During the spring (2019), the more suitable conditions were found with increasing concentrations of chlorophyll a (Chl-a) while during the summer (2013) the highest suitability was estimated for concentrations of Chl-a between 0.002 and 0.004 mg L^{-1}. Finally, for water temperature, the most suitable conditions during the spring of 2019 were found between 16 and 17.5 °C while for the summer of 2013, the temperature range offering the more suitable conditions for the cockles was found between 20 and 23 °C. For both seasons, the variables that most contributed to the models' predictions were salinity, time of submersion and current velocity (Fig. 4). On the other hand, the variable that contributed the least was nitrate concentration (summer of 2013) and Chl-a concentration (spring of 2019).

Environmental Suitability – Projected Environmental Conditions

The potential for temporal transferability of the ensemble models varied according to accuracy metrics (Table 2), reaching fair to good performances both for the spring and summer models. The projections of these models according to the four environmental scenarios proposed showed important changes in the habitat suitability of the Ria de Aveiro for the presence of *C. edule* (Supplementary Figures S3 and S4). The differences in the HSI between each scenario and the estimates for the environmental conditions observed in each season were mapped in Figs. 5 and 6.

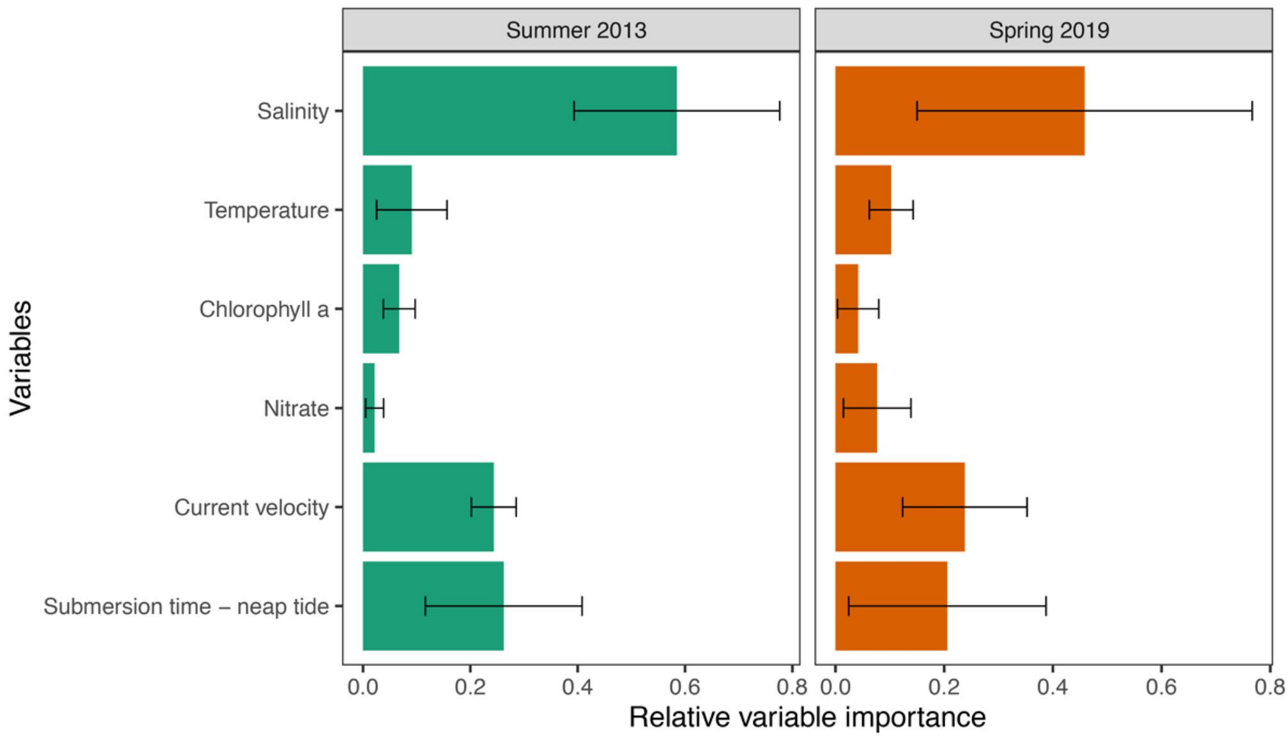

Fig. 4 Mean environmental variable importance (bars) and confidence intervals (whisker) for the models' prediction in the summer of 2013 (green bars) and spring of 2019 (orange bars)

The most severe effects on the habitat suitability for the common cockle were estimated for the scenario of maximum river inflow, resulting in an overall decrease in the HSI, stronger in the model developed for the summer conditions. The few exceptions are observed mostly in areas located in the outermost parts of the Ria. The decrease in the HSI was considerable in some areas compared to the average conditions (differences in HSI > 0.5) and included most of the core habitat regions. For the scenario of low river inflow, extensive areas in the four main channels are also negatively affected, particularly for the model fitted for the spring conditions. However, for the outermost parts of the Ria, an increase in the HSI was estimated in a scenario of low freshwater discharge, stronger for the model fitted for the summer conditions. For the scenario of a 2 °C increase in the average water temperature, the differences between average conditions and model predictions were the smallest compared to the previous two scenarios. For the model fitted for spring, the areas showing a decrease in the HSI include core habitat regions (Mira and S. Jacinto channels, Fig. 2) while an increase in habitat suitability was restricted to fewer and more constricted areas. For the model fitted for summer conditions, the estimates for the scenario of a 2 °C increase in the average water temperature resulted in smaller changes in the HSI and geographically more disperse compared to the model developed for spring. Finally, for the scenario of the combined effect of a 2 °C increased in the seawater temperature and low freshwater discharge, the results between the model fitted for the spring and summer were very distinct. For spring, the model forecasted a stronger degradation in the habitat suitability in the core habitat regions compared to the models testing each scenario independently. On the other hand, the improvement in habitat suitability estimated for the outermost areas of the Ria was lower compared to the prediction made for the scenario of low freshwater discharge. For the model fitted for summer conditions, the results of the combined effect of the 2 °C increase in the water temperature and low freshwater discharge were spatially similar to the results obtained from the scenario of low freshwater discharge but with a lower decrease in the HSI.

Table 2 Assessment of the potential for temporal transferability of the ensemble models developed for the summer of 2013 and spring of 2019 according to three metrics: area under the curve (AUC), sensitivity and Continuous Boyce Index. The AUC and sensitivity average scores were calculated using a cross-validation framework with five independent spatial blocks

Metric	2013	2019
AUC	0.838	0.810
Sensitivity	0.674	0.656
Continuous Boyce Index	0.847	0.886

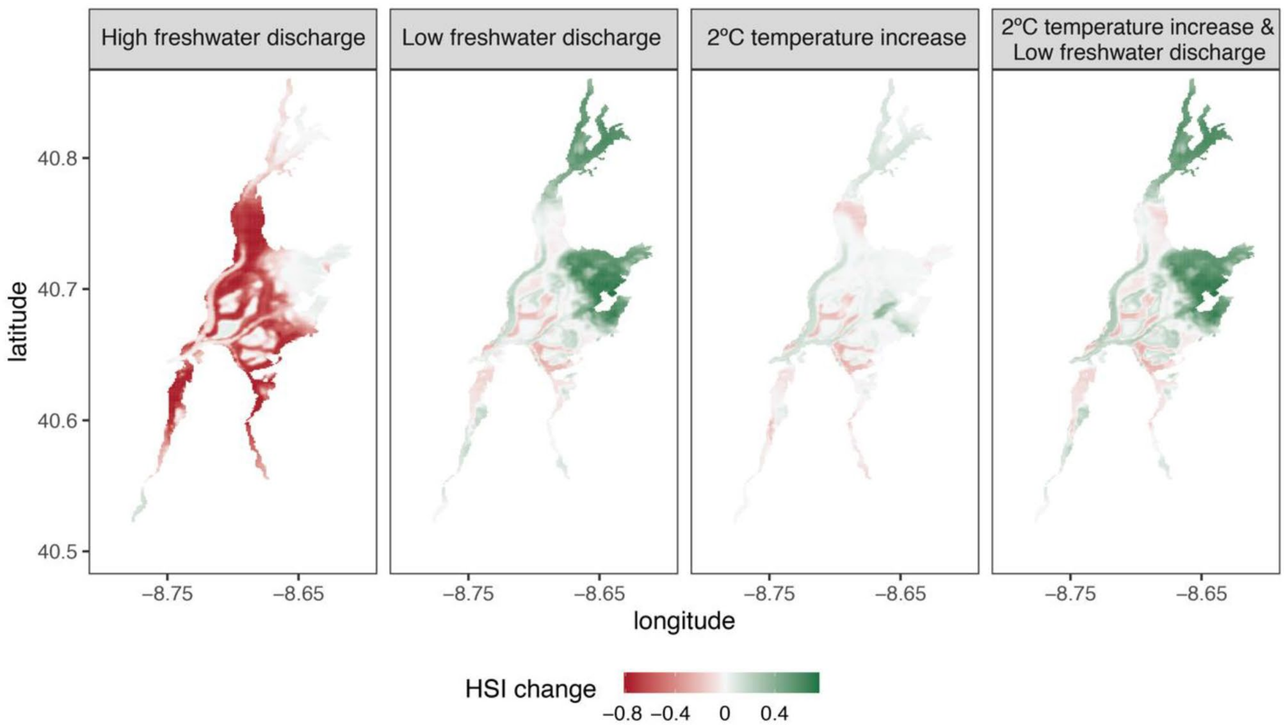

Fig. 5 Change in the habitat suitability index (HSI), expressed as increase/decrease, for each environmental scenario compared with average conditions observed in summer (2013): high freshwater discharge, low freshwater discharge, a 2 °C increase in water temperature and the joint effect of a 2 °C increase in water temperature and low freshwater discharge. Areas colored in different shades of red represent a decrease in HSI while those shaded in green represent an increase in the HSI

Discussion

The fine-scale assessment of habitat suitability within the Ria de Aveiro lagoon for the presence of *C. edule* in the summer of 2013 and spring of 2019 identified large areas of habitat concomitantly classified as highly suitable (i.e., core habitat regions). These regions largely match the locations where the biomass of common cockles reached the highest levels according to the surveys of the GEPETO and COCKLES project campaigns (F. Maia, personal communication). In turn, the model projections suggest that the current distribution of *C. edule* might be affected in the future by the increase in the frequency and intensity of extreme events such as floods, and drought periods combined with heatwaves. The model projections for the scenario of high freshwater discharge forecasted the strongest effects in the HSI of the Ria for the common cockles, with a generalized and considerable decrease in habitat suitability (stronger for the model fitted with summer conditions). For the other scenarios, the projections varied between the models fitted for spring and summer conditions. The largest differences between seasons were estimated for the scenario that tested the combined effect of a 2 °C increase in water temperature and low freshwater discharge. The model fitted for spring conditions predicted more deleterious effects on the HSI, particularly in the core habitat regions, while the model fitted for summer conditions projected mostly an increase of the HSI in the outermost parts of the Ria. The distinct response of the two models (spring and summer conditions) on the joint effect of higher temperature and lower freshwater suggests that the impact of such events on the habitat suitability of the Ria for the presence of cockles may vary depending on season, and how long the projected meteorological conditions last. Despite the euryhaline nature of common cockles and tolerance to temperature fluctuations (Verdelhos et al. 2015a, b), extended changes in the estuarine environment derived from extreme weather events may strongly affect the resilience of the species.

The response curves were identical for the two seasons modeled, except for water temperature and the concentration of Chl-a, likely related to seasonality (Table 1). Verdelhos et al. (2015b) reported the thermal optimum for a population of *C. edule* inhabiting the Mondego estuary (approximately 50 km south of Ria de Aveiro) between 20 and 23 °C, and severe consequences for the survival of cockles at higher temperatures (~ 28 °C). The highest suitability obtained according to the response curves of the models were all observed for temperatures below the 23 °C threshold. The differences observed in the response curves relating to Chl-a concentrations could reflect seasonal

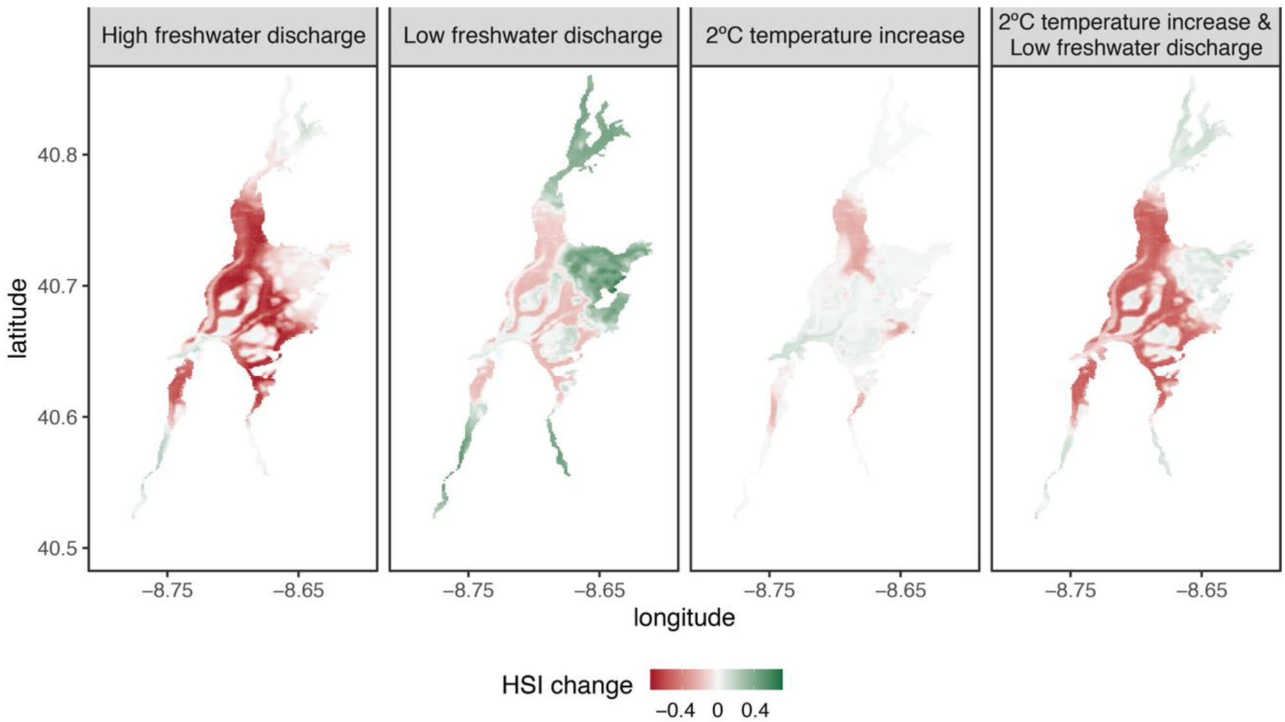

Fig. 6 Change in the habitat suitability index (HSI), expressed as increase/decrease, for each environmental scenario compared with average conditions observed in spring (2019): high freshwater discharge, low freshwater discharge, a 2 °C increase in water temperature and the joint effect of a 2 °C increase in water temperature and low freshwater discharge. Areas colored in different shades of red represent a decrease in HSI while those shaded in green represent an increase in the HSI

patterns of primary production productivity, coinciding with the greater feeding activity of cockles during spring (Newell and Bayne 1980). Increasing levels of salinity (> 22) offer progressively more suitable conditions for the presence of *C. edule*, in agreement with the literature (e.g., Verdelhos et al. 2015a). Concerning nitrate, the increase in the habitat suitability with increasing concentration of nitrate could be related to the importance of this ion for microphytobenthic communities (Decleyre et al. 2015), which represents a substantial portion of cockles' diet. Regarding current velocity and submersion time, a previous modeling study conducted by Cozzoli et al. (2014), suggested that *C. edule* seems to prefer intermediate submersion periods and moderate hydrodynamic stress. A similar result was obtained in this study with model estimates of higher habitat suitability under submersion periods ranging between 11 and 14 h and current velocities ranging from 0.2 to 0.6 ms^{-1}. Both variables may affect the habitat suitability for the presence of *C. edule* determining, for instance, the amount and duration of food available for feeding (De Montaudouin 1996).

The most suitable areas for *C. edule* presence in Ria de Aveiro coincide with those with low uncertainty in the ensemble models estimates. These areas were defined as core habitat regions and can be particularly valuable for the conservation and management of this species in the study area. Nonetheless, the core habitat regions identified are also the ones where models predicted larger decreases in the HSI during projected weather conditions, threatening the species resilience in the future. We highlight however that these results should be considered with care since they only integrate information from two seasons, therefore requiring studies including broader time periods to confirm this trend.

Previous studies suggest that the common cockle may be severely impacted by the increase in the intensity and frequency of extreme climatic events (Singer et al. 2017; Verdelhos et al. 2015a). Model predictions suggested that salinity plays a major role in habitat suitability for *C. edule* in the Ria de Aveiro. Changes in water salinity promoted by fluctuations of river inflow, particularly an increase in freshwater input, may compromise the organisms' survival (Verdelhos et al. 2015a) and impair individual growth performance (Mahony et al. 2022). Moreover, the changes in habitat suitability will likely affect areas identified as core habitat regions.

The ensemble models used in this study reached high predictive performance for average conditions and model response curves coincided with accepted salinity tolerance limits for *C. edule* (Verdelhos et al. 2015a). Hence, this methodology offers an efficient way to produce continuous and spatially explicit information on the distribution of species inhabiting estuary ecosystems from irregular presence data. Also, this modeling approach can be replicated in other coastal ecosystems with information describing the water body and available, for instance, from numerical models of hydrodynamics and water quality. The ensemble ENM approach is also capable of providing uncertainty estimates of model predictions and allows to project potential impacts on the species potential distribution resulting from, for example, climate change. This information is crucial to supporting well-informed decisions on the management (e.g., fisheries) and conservation (e.g., habitat conservation and restoration) of coastal ecosystems and biodiversity, offering a time- and cost-efficient means to identify areas of particular relevance for the presence of the modeled species.

However, ENM predictions are not free of uncertainty and their ability to forecast changes in species distribution dependent on environmental conditions different from the ones used for the model training is limited (Santini et al. 2021). In fact, the models potential transferability demonstrated lower predictive ability on independent data compared to average conditions. Nevertheless, the accuracy scores obtained when models were fitted with data from another year suggest that trends could still be reliably predicted under different environmental conditions. It is also important to note that our model does not consider, for instance, the potential effect of local scale environmental variation (Zhou et al. 2022) or future natural or anthropogenic alterations of the lagoon morphology (Cozzoli et al. 2014) that may affect the distribution of cockles in the study area. According to the model projections, for the scenarios of low (both seasons) and combined effect of 2 °C increase in water temperature with low freshwater discharge into the Ria (spring), no areas with HSI equal to or greater than 0.8 persist (criteria used to define habitat core regions). Under such conditions, additional conservation and management measures may be required in order to ensure the sustainable exploitation of this living resource in Ria de Aveiro. These findings are particularly relevant considering that the frequency and intensity of floods, drought, and heatwave events are expected to increase (IPCC 2014). On the other hand, the importance of water temperature was a less important factor in model predictions. Eurythermal species like common cockles can survive within a wide temperature range which may partially explain this outcome. The forecast for the scenario of an increase of 2 °C in water temperature modeled independently resulted in less pronounced changes in the HSI compared with the other environmental scenarios. Nonetheless, according to the model fitted for spring conditions, this scenario may also result in extensive areas where a general decrease in the HSI may be experienced, particularly in the S. Jacinto channel.

The ENM approach followed in this work predicted substantial changes in the potential distribution of *C. edule* in the Ria de Aveiro under different environmental conditions such as the ones resulting from floods, droughts, and heatwaves. These findings are relevant for fisheries and conservation managers since they may assist the development of future conservation and management measures aiming to preserve this species in the study area. These measures may include limiting the cockles fishery during unfavorable environmental conditions, particularly in the most vulnerable areas to changes in the habitat conditions. Also, the impacts of projected weather events on the occurrence and survival of common cockles go beyond socioeconomic aspects considering the key role that this species has in estuarine ecosystems. In addition to impacts on the species spatial distribution, the increasing intensity and frequency of extreme weather events may also change the functioning of ecosystems and services delivered by cockles and other species that depend on them.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-022-01136-z.

Acknowledgements The authors are grateful to Anthony Peter Moreira for correcting the English and to anonymous reviewers for pertinent suggestions to improve the manuscript.

Funding This work was performed in the scope of the project COACH (cooperative approach applied to conservation and management of cockles), supported by the Ocean Conservation FUND, from Oceanário de Lisboa and Oceano Azul Foundation. Thanks are also due to FCT/MCTES for the financial support to CESAM (UIDP/50017/2020 + UIDB/50017/2020 + LA/P/0094/2020) through national funds. Luísa Magalhães benefited from a research position funded by FEDER through COMPETE2020-POCI and by national funds through FCT/MCTES (POCI-01–0145-FEDER-028425) under the project BISPECIAl (PTDC/CTA-AMB/28425/2017).

References

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43: 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Araújo, M.B., and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22: 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Araújo, M.B., R.J. Whittaker, R.J. Ladle, and M. Erhard. 2005. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecol Biogeogr* 14: 529–538. https://doi.org/10.1111/j.1466-822x.2005.00182.x.

Assis, J., E.A. Serrão, C.M. Duarte, E. Fragkopoulou, and D. Krause-Jensen. 2022. Major expansion of marine forests in a warmer arctic. *Frontiers in Marine Science* 9. https://doi.org/10.3389/fmars.2022.850368.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological*

Modelling 157: 281–300. https://doi.org/10.1016/s0304-3800(02)00200-4.
Braga, H.O., U.M. Azeiteiro, A. Schiavetti, and L. Magalhães. 2022. Checking the changes over time and the impacts of COVID-19 on cockle (Cerastoderma edule) small-scale fisheries in Ria de Aveiro coastal lagoon. *Portugal. Mar Policy* 135: 104843. https://doi.org/10.1016/j.marpol.2021.104843.
Callaway, R., D. Burdon, A. Deasey, K. Mazik, and M. Elliott. 2013. The riddle of the sands: How population dynamics explains causes of high bivalve mortality. *Journal of Applied Ecology* 50: 1050–1059. https://doi.org/10.1111/1365-2664.12114.
Carss, D.N., A.C. Brito, P. Chainho, A. Ciutat, X. De Montaudouin, R.M.F. Otero, M.I. Filgueira, A. Garbutt, M.A. Goedknegt, S.A. Lynch, K.E. Mahony, O. Maire, S.K. Malham, F. Orvain, A. van der Olivier, and S., Jones, L.,. 2020. Ecosystem services provided by a non-cultured shellfish species: The common cockle Cerastoderma edule. *Marine Environment Research* 158: 104931. https://doi.org/10.1016/j.marenvres.2020.104931.
Cozzoli, F., T.G. da Conceição, J.V. Dalen, X. Fang, V. Gjoni, P.M.J. Herman, Z. Hu, L.M. Soissons, B. Walles, T. Ysebaert, and T.J. Bouma. 2020. Biological and physical drivers of bio-mediated sediment resuspension: A flume study on Cerastoderma edule. *Estuarine, Coastal and Shelf Science* 241: 106824. https://doi.org/10.1016/j.ecss.2020.106824.
Cozzoli, F., M. Eelkema, T.J. Bouma, T. Ysebaert, V. Escaravage, and P.M.J. Herman. 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.
Dairain, A., O. Maire, G. Meynard, A. Richard, T. Rodolfo-Damiano, and F. Orvain. 2020. Sediment stability: Can we disentangle the effect of bioturbating species on sediment erodibility from their impact on sediment roughness? *Marine Environment Research* 162: 105147. https://doi.org/10.1016/j.marenvres.2020.105147.
De Montaudouin, X. 1996. Factors involved in growth plasticity of cockles Cerastoderma edule (L.), identified by field survey and transplant experiments. *Journal of Sea Research* 36: 251–265. https://doi.org/10.1016/s1385-1101(96)90794-7.
De Montaudouin, X., and G. Bachelet. 1996. Experimental evidence of complex interactions between biotic and abiotic factors in the dynamics of an intertidal population of the bivalve Cerastoderma edule. Oceanologica Acta, Oceanologica Acta 19.
Decleyre, H., K. Heylen, K. Sabbe, B. Tytgat, D. Deforce, F.V. Nieuwerburgh, C.V. Colen, and A. Willems. 2015. A doubling of microphytobenthos biomass coincides with a tenfold increase in denitrifier and total bacterial abundances in intertidal sediments of a temperate estuary. *PLoS ONE* 10: e0126583. https://doi.org/10.1371/journal.pone.0126583.
Deltares, 2014. Delft3d-FLOW. Simulation of multi-dimensional hydrodynamic flows and transport phenomena, including sediments - User Manual.
Di Cola, V., O. Broennimann, B. Petitpierre, F.T. Breiner, M. D'Amen, C. Randin, R. Engler, J. Pottier, D. Pio, A. Dubuis, L. Pellissier, R.G. Mateo, W. Hordijk, N. Salamin, and A. Guisan. 2017. ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40: 774–787. https://doi.org/10.1111/ecog.02671.
Dias, J., and S. Mariano. 2011. Numerical modelling of hydrodynamic changes induced by a jetty extension – the case of Ria de Aveiro (Portugal). *Journal of Coastal Research* 1008.
Dias, J.M. 2001. Contribution to the study of the Ria de Aveiro hydrodynamics.
Dias, J.M., J. Lopes, and I. Dekeyser. 1999. Hydrological characterisation of Ria de Aveiro, Portugal, in early summer. *Oceanologica Acta* 22: 473–485. https://doi.org/10.1016/s0399-1784(00)87681-1.
Dias, J.M., J.F. Lopes, and I. Dekeyser. 2000. Tidal propagation in Ria de Aveiro Lagoon, Portugal. *Phys Chem Earth Part B Hydrology Oceans Atmosphere* 25: 369–374. https://doi.org/10.1016/s1464-1909(00)00028-9.
Dias, J.M., F. Pereira, A. Picado, C.L. Lopes, J.P. Pinheiro, S.M. Lopes, and P.G. Pinho. 2021. A comprehensive estuarine hydrodynamics-salinity study: Impact of morphologic changes on Ria de Aveiro (Atlantic Coast of Portugal). *J Mar Sci Eng* 9: 234. https://doi.org/10.3390/jmse9020234.
Elith, J., S. Ferrier, F. Huettmann, and J. Leathwick. 2005. The evaluation strip: A new and robust method for plotting predicted responses from species distribution models. *Ecological Modelling* 186: 280–289. https://doi.org/10.1016/j.ecolmodel.2004.12.007.
Elith, J., J.R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.
Guisan, A., R. Tingley, J.B. Baumgartner, I. Naujokaitis-Lewis, P.R. Sutcliffe, A.I.T. Tulloch, T.J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T.G. Martin, J.R. Rhodes, R. Maggini, S.A. Setterfield, J. Elith, M.W. Schwartz, B.A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M.R. Kearney, H.P. Possingham, and Y.M. Buckley. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435. https://doi.org/10.1111/ele.12189.
Gutiérrez, J.M., R.G. Jones, G.T. Narisma, L.M. Alves, M. Amjad, V. IGorodetskaya, M. Grose, N.A.B. Klutse, S. Krakovska, J. Li, D. Martínez-Castro, L.O. Mearns, S.H. Mernild, T. Ngo-Duc, B. van den Hurk, and J.-H. Yoon. 2021. Atlas. In climate change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., and Zhou, B. (eds.)]. Cambridge University Press. In Press. Interactive Atlas available from Available from http://interactive-atlas.ipcc.ch/.
Hastie, T., R. Tibshirani, and A. Buja. 1994. Flexible discriminant analysis by optimal scoring. *Journal of American Statistical Association* 89: 1255–1270. https://doi.org/10.1080/01621459.1994.10476866.
Hastie, T., R. Tibshirani, and J. Friedman. 2009. The Elements of Statistical Learning, Data Mining, Inference, and Prediction. *Springer Ser Statistics*. https://doi.org/10.1007/978-0-387-84858-7.
Hayward, P.J., and J.S. Ryland. 1995. *Marine fauna of the British Isles and North-West Europe*. Clarendon Press.
Hiemstra, P.H., E.J. Pebesma, C.J.W. Twenhöfel, and G.B.M. Heuvelink. 2009. Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers & Geosciences* 35: 1711–1721. https://doi.org/10.1016/j.cageo.2008.10.011.
Hirzel, A.H., G.L. Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.
Iglesias, J.I.P., and E. Navarro. 1991. Energetics of growth and reproduction in cockles (Cerastoderma edule): Seasonal and age-dependent variations. *Marine Biology* 111: 359–368. https://doi.org/10.1007/bf01319407.
INE. 2020. Fisheries statistics reports. INE - Instituto Nacional de Estatística, Lisboa, Portugal.
IPCC. 2014. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [WWW Document].

https://epic.awi.de/id/eprint/37530/1/IPCC_AR5_SYR_Final.pdf (accessed 1.6.22).

Kater, B., A.G. van Kessel, and J. Baars. 2006. Distribution of cockles Cerastoderma edule in the Eastern Scheldt: Habitat mapping with abiotic variables. *Marine Ecology Progress Series* 318: 221–227. https://doi.org/10.3354/meps318221.

Lauria, V., A.M. Power, C. Lordan, A. Weetman, and M.P. Johnson. 2015. Spatial transferability of habitat suitability models of Nephrops norvegicus among fished areas in the Northeast Atlantic: Sufficiently stable for marine resource conservation? *PLoS ONE* 10: e0117006. https://doi.org/10.1371/journal.pone.0117006.

Leroy, B., C.N. Meynard, C. Bellard, and F. Courchamp. 2016. virtualspecies, an R package to generate virtual species distributions. *Ecography* 39: 599–607. https://doi.org/10.1111/ecog.01388.

Lopes, C.L., S. Plecha, P.A. Silva, and J.M. Dias. 2013. Influence of morphological changes in a lagoon flooding extension: Case study of Ria de Aveiro (Portugal). *Journal of Coastal Research* 65: 1158–1163. https://doi.org/10.2112/si65-196.1.

Mahony, K.E., S. Egerton, S.A. Lynch, H. Blanchet, M.A. Goedknegt, E. Groves, N. Savoye, X. De Montaudouin, S.K. Malham, and S.C. Culloty. 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.

Mahony, K.E., S.A. Lynch, S. Egerton, S. Cabral, X. De Montaudouin, A. Fitch, L. Magalhães, M. Rocroy, and S.C. Culloty. 2020. Mobilisation of data to stakeholder communities. Bridging the research-practice gap using a commercial shellfish species model. *Plos One* 15: e0238446. https://doi.org/10.1371/journal.pone.0238446.

Maia, F., C.M. Barroso, and M.B. Gaspar. 2021. Biology of the common cockle Cerastoderma edule (Linnaeus, 1758) in Ria de Aveiro (NW Portugal): Implications for fisheries management. *Journal of Sea Research* 171: 102024. https://doi.org/10.1016/j.seares.2021.102024.

Melo-Merino, S.M., H. Reyes-Bonilla, and A. Lira-Noriega. 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.

Moreira, M.H., H. Queiroga, M.M. Machado, and M.R. Cunha. 1993. Environmental gradients in a southern Europe estuarine system: Ria de Aveiro, Portugal implications for soft bottom macrofauna colonization. *Netherland J Aquat Ecol* 27: 465–482. https://doi.org/10.1007/bf02334807.

Naimi, B., and M.B. Araújo. 2016. sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography* 39: 368–375. https://doi.org/10.1111/ecog.01881.

Newell, R.I.E., and B.L. Bayne. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle Cardium (=Cerastoderma) edule (Bivalvia: Cardiidae). *Marine Biology* 56: 11–19. https://doi.org/10.1007/bf00390589.

Peteiro, L.G., S.A. Woodin, D.S. Wethey, D. Costas-Costas, A. Martínez-Casal, C. Olabarria, and E. Vázquez. 2018. Responses to salinity stress in bivalves: Evidence of ontogenetic changes in energetic physiology on Cerastoderma edule. *Sci Rep-Uk* 8: 8329. https://doi.org/10.1038/s41598-018-26706-9.

Peterson, A.T., M. Papeş, and J. Soberón. 2015. Mechanistic and correlative models of ecological niches. *European J Ecol* 1: 28–38. https://doi.org/10.1515/eje-2015-0014.

Picado, A., J.M. Dias, and A.B. Fortunato. 2010. Tidal changes in estuarine systems induced by local geomorphologic modifications. *Continental Shelf Research* 30: 1854–1864. https://doi.org/10.1016/j.csr.2010.08.012.

Rakotomalala, C., K. Grangeré, M. Ubertini, M. Forêt, and F. Orvain. 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.

Ramón, M. 2003. Population dynamics and secondary production of the cockle Cerastoderma edule (L.) in a backbarrier tidal flat in the Wadden Sea. *Scientia Marina* 67:429–443. https://doi.org/10.3989/scimar.2003.67n4429.

Reiss, H., S. Birchenough, A. Borja, L. Buhl-Mortensen, J. Craeymeersch, J. Dannheim, A. Darr, I. Galparsoro, M. Gogina, H. Neumann, J. Populus, A.M. Rengstorf, M. Valle, G. van Hoey, M.L. Zettler, and S. Degraer. 2014. Benthos distribution modelling and its relevance for marine ecosystem management. *ICES Journal of Marine Science* 72: 297–315. https://doi.org/10.1093/icesjms/fsu107.

Rullens, V., F. Stephenson, A.M. Lohrer, M. Townsend, and C.A. Pilditch. 2021. Combined species occurrence and density predictions to improve marine spatial management. *Ocean Coast Manage* 209: 105697. https://doi.org/10.1016/j.ocecoaman.2021.105697.

Saito, T., and M. Rehmsmeier. 2017. Precrec: Fast and accurate precision–recall and ROC curve calculations in R. *Bioinformatics* 33: 145–147. https://doi.org/10.1093/bioinformatics/btw570.

Santini, L., A. Benítez-López, L. Maiorano, M. Čengić, and M.A.J. Huijbregts. 2021. Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions* 27: 1035–1050. https://doi.org/10.1111/ddi.13252.

Sequeira, A.M.M., P.J. Bouchet, K.L. Yates, K. Mengersen, and M.J. Caley. 2018. Transferring biodiversity models for conservation: Opportunities and challenges. *Methods in Ecology and Evolution* 9: 1250–1264. https://doi.org/10.1111/2041-210x.12998.

Singer, A., G. Millat, J. Staneva, and I. Kröncke. 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, L.M., T.G. da Conceiçâo, J. Bastiaan, J. van Dalen, T. Ysebaert, P.M.J. Herman, F. Cozzoli, and T.J. Bouma. 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.

Stefanova, A., V. Krysanova, C. Hesse, and A.I. Lillebø. 2015. Climate change impact assessment on water inflow to a coastal lagoon: the Ria de Aveiro watershed, Portugal. *Hydrological Sciences Journal* 141217125340005.https://doi.org/10.1080/02626667.2014.983518.

Tebble, N. 1966. British bivalve seashells. A handbook for identification. Trustees of the British Museum (Natural History), London, UK.

Thuiller, W., B. Lafourcade, R. Engler, and M.B. Araújo. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32: 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.

Tommasi, D., C.A. Stock, M.A. Alexander, X. Yang, A. Rosati, and G.A. Vecchi. 2017. Multi-annual climate predictions for fisheries: An assessment of skill of sea surface temperature forecasts for large marine ecosystems. *Frontiers Mar Sci* 4: 201. https://doi.org/10.3389/fmars.2017.00201.

Urban, M.C., G. Bocedi, A.P. Hendry, J.-B. Mihoub, G. Pe'er, A. Singer, J.R. Bridle, L.G. Crozier, L.D. Meester, W. Godsoe, A. Gonzalez, J.J. Hellmann, R.D. Holt, A. Huth, K. Johst, C.B. Krug, P.W. Leadley, S.C.F. Palmer, J.H. Pantel, A. Schmitz, P.A. Zollner, and J.M.J. Travis. 2016. Improving the forecast for biodiversity under climate change. *Science* 353: 1113-+. https://doi.org/10.1126/science.aad8466.

Valavi, R., J. Elith, J.J. Lahoz-Monfort, and G. Guillera-Arroita. 2019. blockCV: An r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution* 10: 225–232. https://doi.org/10.1111/2041-210x.13107.

Van der Schatte Olivier, A., L. Jones, L.L. Vay, M. Christie, J. Wilson, and S.K. Malham. 2018. A global review of the ecosystem services provided by bivalve aquaculture. *Rev Aquacult* 12: 3–25. https://doi.org/10.1111/raq.12301.

Vargas, C.I.C., N. Vaz, and J.M. Dias. 2017. An evaluation of climate change effects in estuarine salinity patterns: Application to Ria de Aveiro shallow water system. *Estuarine, Coastal and Shelf Science* 189: 33–45. https://doi.org/10.1016/j.ecss.2017.03.001.

Vaz, L., M. Mateus, J. Serôdio, J.M. Dias, and N. Vaz. 2016. Primary production of the benthic microalgae in the bottom sediments of Ria de Aveiro lagoon. *Journal of Coastal Research* 75: 178–182. https://doi.org/10.2112/si75-36.1.

Vaz, N., J.M. Dias, P. Leitão, and I. Martins. 2005. Horizontal patterns of water temperature and salinity in an estuarine tidal channel: Ria de Aveiro. *Ocean Dynam* 55: 416–429. https://doi.org/10.1007/s10236-005-0015-4.

Vaz, N., J.M. Dias, and P.C. Leitão. 2009. Three-dimensional modelling of a tidal channel: The Espinheiro Channel (Portugal). *Continental Shelf Research* 29: 29–41. https://doi.org/10.1016/j.csr.2007.12.005.

Vaz, N., L. Vaz, J. Serôdio, and J.M. Dias. 2019. A modeling study of light extinction due to cohesive sediments in a shallow coastal lagoon under well mixed conditions. *Science of the Total Environment* 694: 133707. https://doi.org/10.1016/j.scitotenv.2019.133707.

Verdelhos, T., J.C. Marques, and P. Anastácio. 2015a. The impact of estuarine salinity changes on the bivalves Scrobicularia plana and Cerastoderma edule, illustrated by behavioral and mortality responses on a laboratory assay. *Ecological Indicators* 52: 96–104. https://doi.org/10.1016/j.ecolind.2014.11.022.

Verdelhos, T., J.C. Marques, and P. Anastácio. 2015b. Behavioral and mortality responses of the bivalves Scrobicularia plana and Cerastoderma edule to temperature, as indicator of climate change's potential impacts. *Ecological Indicators* 58: 95–103. https://doi.org/10.1016/j.ecolind.2015.05.042.

Yates, K.L., P.J. Bouchet, M.J. Caley, K. Mengersen, C.F. Randin, S. Parnell, A.H. Fielding, A.J. Bamford, S. Ban, A.M. Barbosa, C.F. Dormann, J. Elith, C.B. Embling, G.N. Ervin, R. Fisher, S. Gould, R.F. Graf, E.J. Gregr, P.N. Halpin, R.K. Heikkinen, S. Heinänen, A.R. Jones, P.K. Krishnakumar, V. Lauria, H. Lozano-Montes, L. Mannocci, C. Mellin, M.B. Mesgaran, E. Moreno-Amat, S. Mormede, E. Novaczek, S. Oppel, G.O. Crespo, A.T. Peterson, G. Rapacciuolo, J.J. Roberts, R.E. Ross, K.L. Scales, D. Schoeman, P. Snelgrove, G. Sundblad, W. Thuiller, L.G. Torres, H. Verbruggen, L. Wang, S. Wenger, M.J. Whittingham, Y. Zharikov, D. Zurell, and A.M.M. Sequeira. 2018. Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution* 33: 790–802. https://doi.org/10.1016/j.tree.2018.08.001.

Zhou, Z., T.J. Bouma, G.S. Fivash, T. Ysebaert, and IJzerloo, L. van, Dalen, J. van, Dam, B. van, 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.