Vulnerability of Zostera noltei to Sea Level Rise: the Use of Clustering Techniques in Climate Change Studies

7 authors, including:

Bárbara Ondiviela
Universidad de Cantabria
54 PUBLICATIONS   **1,680** CITATIONS

SEE PROFILE

Cristina Galván
IHCantabria - Instituto de Hidráulica Ambiental de la Universidad de Cantabria, S…
21 PUBLICATIONS   **918** CITATIONS

SEE PROFILE

Maria Recio
Universidad de Cantabria
16 PUBLICATIONS   **385** CITATIONS

SEE PROFILE

Mirian Jiménez
Universidad de Cantabria
7 PUBLICATIONS   **98** CITATIONS

SEE PROFILE

Vulnerability of Zostera noltei *to Sea Level Rise: the Use of Clustering Techniques in Climate Change Studies*

Bárbara Ondiviela, Cristina Galván, María Recio, Mirian Jiménez, José Antonio Juanes, Araceli Puente & Inigo J. Losada

ONLINE
FIRST

Springer

Springer

Vulnerability of *Zostera noltei* to Sea Level Rise: the Use of Clustering Techniques in Climate Change Studies

Bárbara Ondiviela[1] · Cristina Galván[1] · María Recio[1] · Mirian Jiménez[1] · José Antonio Juanes[1] · Araceli Puente[1] · Inigo J. Losada[1]

Abstract

The effects of sea level rise are now beginning to be detected in seagrass ecosystems. The present work deals with how sea level rise translates into changes on seagrass distribution at local scale and how to provide reliable information and tools to predict the vulnerability of shallow coastal ecosystems to the expected effects. To evaluate mid- and long-term changes in the habitat suitability of *Zostera noltei* a combination of clustering techniques—Self organizing maps and *K* means—considering RCP and high-end projections was used. The study, developed at the Bay of Santander, provides evidence indicating that sea level rise will highly affect meadows of *Zostera noltei*. This species will experience an important spatial variability, mainly in deeper areas, where moderate rising levels will substantially reduce the availability of suitable habitats for this species. This process will intensify over time and seagrass meadows are expected to be severely affected in the long term. A rising level of 0.63 m by 2100 will result in a 14.2% reduction in suitable habitats, while a 51% loss will occur with a sea level rise of 2 m. Our results indicate that large areas of seagrass in the Bay of Santander will be lost with future sea level rise, especially in the absence of major changes to sediment dynamics. However, a review of the main feedbacks and self-amplifying mechanisms regulating their adaptation allows us to be confident about *Zostera noltei's* capacity to adapt to changing conditions in the near future. In the long term, there are more doubts regarding this ability and possible responses remain highly uncertain.

Keywords Seagrasses · SOMs · *K* means · Habitat suitability · Bay of Biscay · Bay of Santander

Introduction

Eelgrass (*Zostera noltei*) beds are the dominant perennial vegetation in soft-sediment marine estuaries along the European Atlantic Coast. They are habitat-forming ecosystem engineers that play a relevant role in ecological, physical and chemical processes and provide highly valuable ecosystem services (Ondiviela et al. 2014). As natural and anthropogenic threats in coastal areas continue to grow, so do concerns about their impact on the associated ecosystems (Frau et al. 2014; Traboni et al. 2018). Of particular importance is the impact of sea level rise in low-lying coastlines. *Z. noltei* can be highly persistent in pristine environments, but slight changes in sea levels may trigger major consequences to this species' distribution. Assessing the magnitude of these changes remains a challenge, and evidence regarding whether seagrasses can actually

---

Communicated by: Melisa C. Wong

✉ Bárbara Ondiviela
  ondiviela@unican.es

  Cristina Galván
  cristina.galvan@unican.es

  María Recio
  reciom@unican.es

  Mirian Jiménez
  mirian.jimenez@unican.es

  José Antonio Juanes
  juanesj@unican.es

  Araceli Puente
  puentea@unican.es

  Inigo J. Losada
  inigo.losada@unican.es

[1] Environmental Hydraulics Institute, Universidad de Cantabria, Avda. Isabel Torres, 15, Parque Científico y Tecnológico de Cantabria, 39011 Santander, Spain

⌂ Springer

adapt to sea level rise is still inconclusive and highly site-specific (De los Santos et al. 2019; Kairis and Rybczyk 2010; Shaughnessy et al. 2012; Spalding et al. 2014; Valle et al. 2014). Therefore, for these species to persist in the mid and long term, a better understanding of how sea level rise is impacting eelgrass beds and how to assess changes over space and time is a core requirement. Currently, changes in marine ecosystems are predominately obtained through broad-spectrum Species Distribution Models (SDM). They relate species' field observations to environmental predictor variables (Guisan et al. 2017) to derive the species' distribution. SDM are commonly used because of their relative ease of use and availability (Calleja 2019). However, they present limitations for analyzing variations in species' distributions due to local environmental changes, and applications in estuarine environments at local scales are still scarce (e.g. De la Hoz et al. 2018; Frau et al. 2014; Valle et al. 2014).

On the other hand, clustering techniques look for patterns, extracting features from the original data using iterative learning algorithms, which include self-organizing neighbourhood mechanisms. In essence, they organize objects into groups whose members are similar in some way. At the local scale, where species-environment relationships are strongly scale dependent (Fournier et al. 2017), and where neighbourhood relationships are highly relevant in the definition of spatial patterns, clustering techniques may provide reliable information. Clustering is a common technique in statistical data analysis, used in many fields (i.e. machine learning, pattern recognition, image analysis, information retrieval, bioinformatics). It has been extensively applied to a variety of problems in the biological and ecological domains (Céréghino et al. 2005; de la Hoz et al. 2017; Hopton and Mayer 2006; Mele and Crowley 2008; Ohlson et al. 2006; Russo et al. 2014; Weber et al. 2011), but, to our knowledge, has not be used previously to analyze how sea level rise may trigger changes in the distribution of marine ecosystems at the local scale. This work explores the use of these techniques to create suitability maps to evaluate the vulnerability of Z. noltei to sea level rise in the mid and long terms (2065 and 2100), considering the RCP projections of mean sea level rise and a high-end 2-m rise scenario.

Methodology

Study Area

The Bay of Santander (Bay of Biscay) is a medium-sized estuary (2270 ha) confined by a sandy spit in the mouth (6 km). Because of the natural shelter offered from waves, the main hydrodynamic forces at the estuary are tides and currents (Fig. 1). The Bay is a meso-tidal (2.8 m of mean tidal range) and well-mixed estuary, with maximum current velocities (0.8 $m^3 s^{-1}$) at the mouth (Ondiviela et al. 2015). The main freshwater input is from the Miera River (average flow 8.2 $m^3 s^{-1}$), which strongly influences local biological and physical dynamics. The estuary contains large extensions of tidal flats (65% of total surface), occupied by Z. noltei, and subtidal areas occupied by Zostera marina.

Creation of Suitability Maps

Explanatory Variables

The methodology was trained with a selection of explanatory variables identified to be important for the distribution of seagrasses in well-mixed sheltered estuarine embayments (Charpentier et al. 2005; Davis et al. 2016). The variables selected were maximum current velocity (m/s), water column height (m), emerged time (h/half tidal cycle) and sand content (%). Currents and substratum are important factors controlling seagrass growth (Greve and Binzer 2004; Koch 2001). The height of the water column establishes the lower depth limit (as a biological surrogate of the light available during high tide) and emerged time defines the depth distribution limit between Z. noltei (shallow) and Z. marina (deep), as a surrogate of the competition interactions between the two species.

Current velocity, water column height and emerged time were modelled for the reference year (2012) using a two-dimensional hydrodynamic model (H2D) which resolves the well-known vertical-averaged shallow water equations (Galván et al. 2010). The model provides water elevation and depth-averaged velocity as a function of the propagation of the astronomic tide and river inflow into the estuary. A simulation of 15 days during spring tides (March 2012) was carried out considering the astronomic tide and the average annual flow of the Miera River. These tides, characterized by a high variability in water level, may have an important effect on tidal vegetation. Bathymetry data from the estuary and adjacent coastal areas were used to produce a high-resolution grid of 415 × 460 cells with a 51 × 51-m cell length.

The model was calibrated with two parameter values which are extensively used in estuaries in Northern Spain (Galván et al. 2010): the Chézy coefficient given by the Colebrook-White equation (bottom roughness = 0.2), and the eddy viscosity coefficient (10 m^2/s). Emerged time was calculated as the average time (h) every half tidal cycle (6 h). Water column height and current velocity were defined as the average of the maximum values recorded at each individual tidal cycle. Grain size was obtained from 69 sampling sites collected from 2001 to 2012 and interpolated by weighted inverse distance, using barrier polyline interpolation. To ensure that the four explanatory variables were not highly correlated and avoid
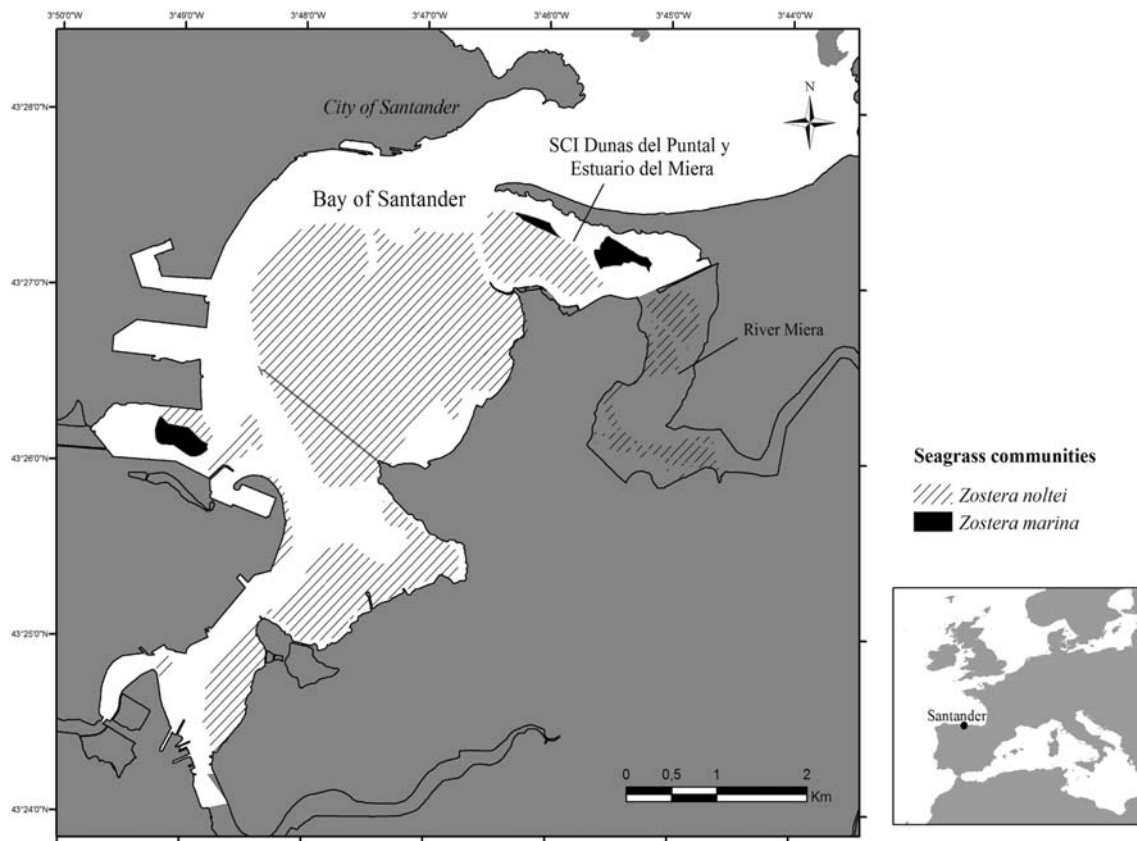
Fig. 1 Distribution of seagrasses *Zostera noltei* and *Zostera marina* in the Bay of Santander (year 2012)

data redundancy, the Spearman's non-parametric rank-correlation method was used with a value of $\rho < 0.85$.

Clustering Analysis

Self-Organizing Maps (SOMs) and K means were combined to create a suitability map of *Z. noltei* for the year 2012 (reference condition map). Beds of *Z. noltei* are monospecific and the habitat was mapped through a species-level modelling approach. Once the hydromorphological and geophysical data were normalized and standardized, SOMs were randomly initialised. The model was trained using an iterative learning algorithm, which included a self-organizing neighbourhood mechanism. This means that neighbouring groups in the resulting 2-D reticule are also similar in real space (Jiménez et al. 2012). The input layer for each variable was integrated by 7.784 cells and the output layer by 49 centroids arranged in a heptagonal reticule (7×7), where each cell's datum was assigned to a certain centroid (Jiménez et al. 2012). The dimension of the reticule was determined by the size of the grid and the four chosen explanatory variables. A frequency matrix representing the probability of the corresponding combination of hydromorphological and geophysical conditions in each centroid was created.

The K means test, initialized with the maximum dissimilarity algorithm, was applied to cluster the trained map obtained from SOMs into three habitat suitability categories (e.g. Camus et al. 2011; Solidoro et al. 2007). K means clustering was carried out with five input variables for each centroid: the mean value of the four explanatory variables previously used for the SOM analysis and the records of *Z. noltei* (35% of the records, randomly selected from the field map collected in 2012). As a result, the centroids obtained in the SOM were classified into three probability groups, that were linked to different habitat suitability conditions: Favourable suitability (high probability of occurrence); stressful suitability (moderate probability of occurrence); and unfavourable suitability (low probability of occurrence). The groups obtained in the K means analysis were represented geographically to obtain the suitability map of *Z. noltei* in the Bay of Santander.

Validation of Suitability Maps

The accuracy of the resulting suitability map was tested with the field map (65% of the records, randomly selected). The spatial distribution map for the year 2012 (Fig. 1) was obtained from field surveys, through a 1:5000 scale mapping of geo-referenced aerial photographs (year 2010). The unweighted Cohen's Kappa coefficient (Cohen 1960) and the area under

the characteristic curve, AUC (Felicísimo 2011), were calculated to obtain statistical measures of methodology reliability in predicting habitat suitability. Calculations were made considering the predicted suitability (favourable/unfavourable conditions) and species observations (presence/absence). The number of field observations (presence/absence) for the analysis was 2057 for unfavourable, and 1560 for favourable conditions, respectively. The strength of the agreement was assessed by the interpretation of the Kappa index proposed by Monsreud and Leemans (1992). Kappa is dimensionless, ranges from −1 to 1 and increases with the degree of agreement between the two groups analyzed. The AUC gives a measure of predictive sensitivity by comparing the probability of agreement between predictions and outcomes. The AUC analyses the probability that a random false positive and a random true positive are correctly predicted by the model, an AUC value of 0.5 indicating that model predictions are not better than random guessing. Validation was completed with a confusion matrix. To construct this matrix, random points were distributed in the study area. The percentage of successes and failures of the suitability map was estimated by comparing species observations (presence/absence) with the predicted suitability (favourable, stressful and unfavourable).

Vulnerability of *Zostera noltei* to Projected Sea Level Rise Scenarios

Under this study, the vulnerability to sea level rise is understood as the balance between gain and loss of suitable habitats for *Z. noltei* between the projected maps and a given reference year. The implementation performed at the Bay of Santander assessed the vulnerability of *Z. noltei* as changes in habitat suitability between the projections and the reference year (established in 2012). This assessment was run considering only the favourable suitability condition.

Sea Level Rise Simulations

Relative sea level rise downscaled to this region shows very minor deviations from the global mean (Toimil et al. 2017). Thus, for this region, global mean sea level rise (GMSL) scenarios for the lowest and highest trends in CO_2 emissions (RCP 2.6 and 8.5) and mid- and long-term projections of climate change help to understand how rising sea levels translate into changes in species suitability maps (Table 1). Apart from the IPCC scenarios (2013), an additional extreme long-term scenario of 2.0 m rise (H++) was also simulated (Nicholls and Cazenave 2010; Pfeffer et al. 2008; Rahmstorf 2007).

Simulations for the selected scenarios and projections were performed by increasing the average sea level and modelling changes in water column height, emerged time and current velocity (explanatory variables) with the H2D model.

Table 1 Global mean sea level rise considered for two RCP scenarios (IPCC 2013) in the mid and long term and the H++ scenario (Nicholls and Cazenave 2010; Pfeffer et al. 2008; Rahmstorf 2007)

Scenario	2046–2065		2081–2100	
	Mean	Probable range	Mean	Probable range
RCP 2.6	+ 0.24 m	0.17–0.32 m	+ 0.40 m	0.26–0.55 m
RCP 8.5	+ 0.30 m	0.22–0.38 m	+ 0.63 m	0.45–0.82 m
H++			+ 2 m	

Suitability maps for the RCP scenarios were defined considering different categories of habitat suitability within the grid. Each cell of the grid was assigned to the category with the smaller Euclidean distance between the centroid of the *K* means obtained for the year 2012 and the hydromorphological and geophysical conditions of the predicted change.

Vulnerability Assessment

For each scenario and projection of sea level rise (RCP), the vulnerability of *Z. noltei* meadows was estimated as the net loss (or gain) of areas with favourable conditions from the reference year. The magnitude of change (dimensionless value) was calculated with the Index of Relative Change (IRC) according to the approach developed by Frederiksen et al. (2004):

$$IRC = \frac{(loss + gain)}{(loss + gain + no\ change)}$$

Loss, gain and no change refer to the predicted area (ha) under favourable suitability conditions that disappears, is formed or remains equal, from year 1 (reference condition map) to year 2 (horizon of sea level rise projections). The IRC index ranges between 0 (no change) and 1 (complete change). The higher the rate of change (closer to 1), the more vulnerable the meadow. This ratio normalizes seagrass distribution dynamics regardless of the size of the study, or absolute area of change.

Results

Habitat Suitability for *Zostera noltei*

In the SOMs projection space (7 × 7) created for the reference year (2012), there were well-defined gradients for all explanatory variables (Fig. 2a–d). Similar centroids were located adjacent and average values representing each centroid varied smoothly between neighbouring centroids. The centroids in the upper right side of the SOMs maps were characterized by high mean current velocities (0.4 ± 0.08 m/s), water
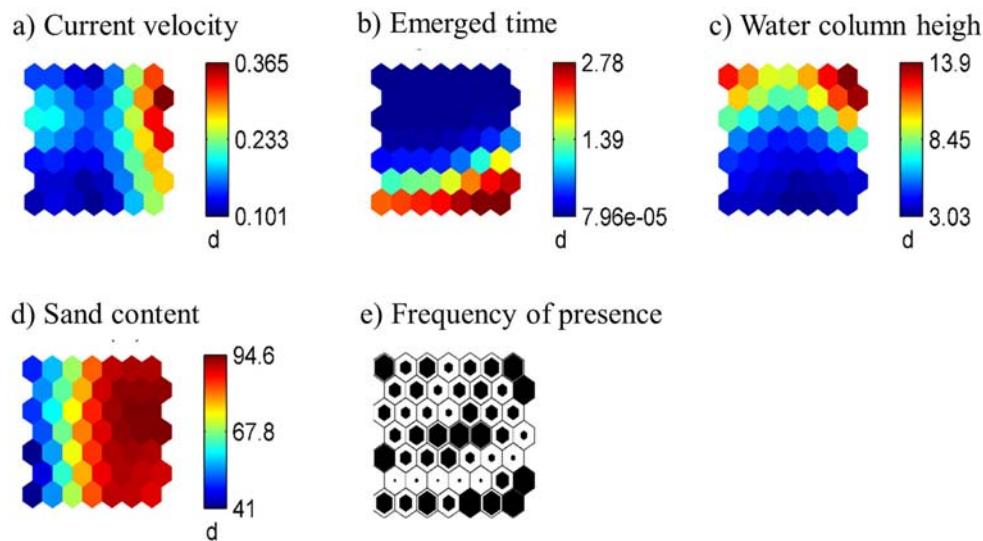
Fig. 2 Visualization of explanatory variables according to SOM maps (49 centroids) and frequency of presence of grid cells in each centroid. Centroids of the trained SOM show the mean value of the explanatory variable: **a** current velocity (m/s); **b** emerged time (h); **c** water column height (m); **d** sand content (%); and **e** frequency matrix representing the probability of the corresponding combination of the four explanatory variables (hydromorphological and geophysical conditions) in each centroid. The probability is indicated by the size of the black dot. Highest probability = black dot; lowest probability = white dot

column height (15.0 ± 0.85 m) and sand content (94.3 ± 7.4%), while centroids with the highest mean emerged time (3.0 ± 0.44 h) appeared in the lower right side of the reticule. The combination of the SOMs for the four variables resulted in a frequency matrix, where each centroid represents the probability of a certain combination of hydromorphological and geophysical conditions (Fig. 2e). The cells of the grid were unevenly distributed throughout the centroids map and the conditions most frequently found were characterized by the following: (1) maximum emerged time and high sand content, which corresponds with the conditions found in tidal flats (lower right side of the reticule); and (2) maximum velocities, column height and sand content, which corresponds with conditions found in water channels (upper right side of the reticule).

Attending to the resulting suitability map, the area with favourable conditions in 2012 was estimated to be 594.8 ha (Fig. 3). Favourable suitability conditions accounted for the areas with the highest probability of species occurrence (60.7% of presence records); stressful suitability areas were characterized by a moderate probability of occurrence (32.5% of records), while unfavourable suitability areas represented those with the lowest probability of seagrass occurrence (6% of records).

Each suitability category was associated with a specific inundation level (emerged time and column height) and sand content, although these variables showed remarkable differences in the range of variation (P75 and P25) within each habitat (Fig. 4). The three categories were described by specific average characteristics. Favourable suitability was characterized by low inundation levels (2.7 h of emerged time and 3.64 m of water column) and high sand content (92.1%). Stressful suitability areas showed a high range of variability as regards emerged time and sand content, while it typically showed a moderate sand content (60.88%), slow current velocities (0.12 m/s) and high emerged time (0.99 h). In general, the average values for the explanatory variables under this category were below the values obtained for the other two categories. Lastly, areas with unfavourable suitability conditions for *Z. noltei* showed high and permanent inundation levels (emerged time, 0.01 h; water column 11.08 m) and high sand contents (9.42%).

Validation of Suitability Maps

The habitat suitability map of *Z. noltei*, developed by the geographical projection of the SOMs reticule, provided a high level of discrimination regarding the presence or absence of *Z. noltei* observations. Compared with the field distribution map, the modelled map predicted presence or absence with a good accuracy (Kappa, 0.7) and sensitivity (AUC, 0.86). The distribution of *Z. noltei* was significantly ($p < 0.05$) explained by the model. Indeed, the species appeared to be absent from most of the area classified as unfavourable (93%) and colonized 76% of the surface classified as favourable for settlement (Table 2). The stressful category was similarly characterized by the absence/presence of the species (53% and 47%, respectively).

Fig. 3 Suitability map of *Zostera noltei* in the Bay of Santander (favourable, stressful and unfavourable suitability categories) for the year 2012 obtained with the *K* means algorithm over the SOMs reticule (7 × 7). The limits of the three habitat categories and the number of records for *Zostera noltei* in each centroid are indicated within the centroids
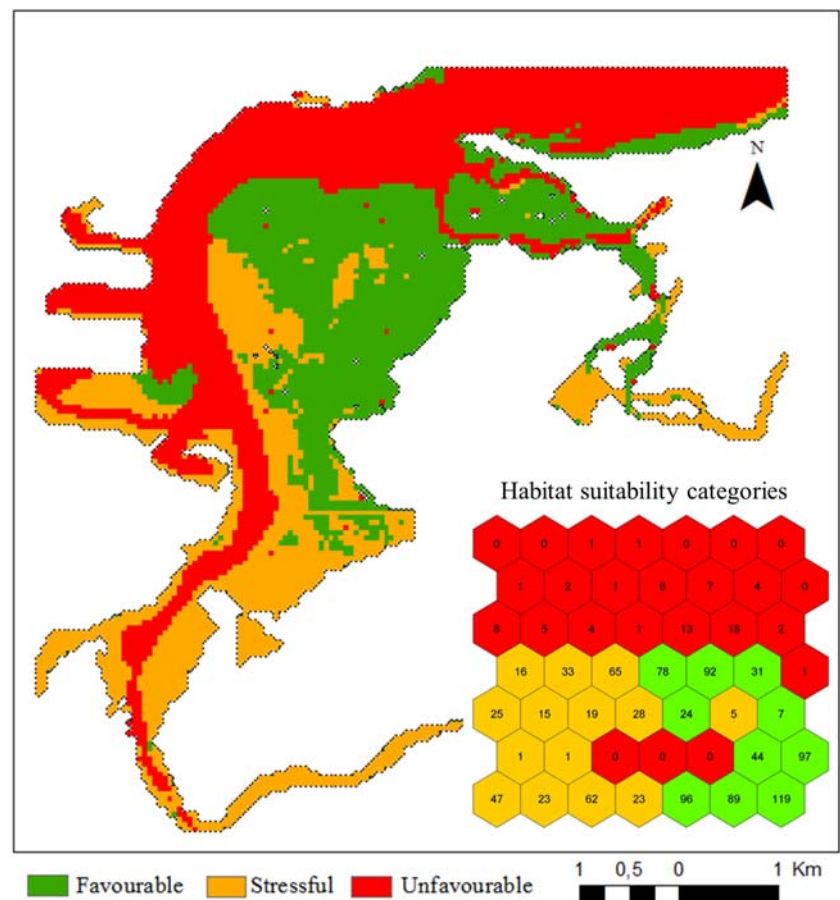

Fig. 4 Habitat characterization for Favourable (F), Stressful (S) and Unfavourable (U) suitability conditions. From left to right, each subplot shows the variance in **a** current velocity, **b** emerged time, **c** water column and **d** sand content for the reference year. Boxes indicate P75, P25 and P50; asterisks (*) indicate maximum and minimum values
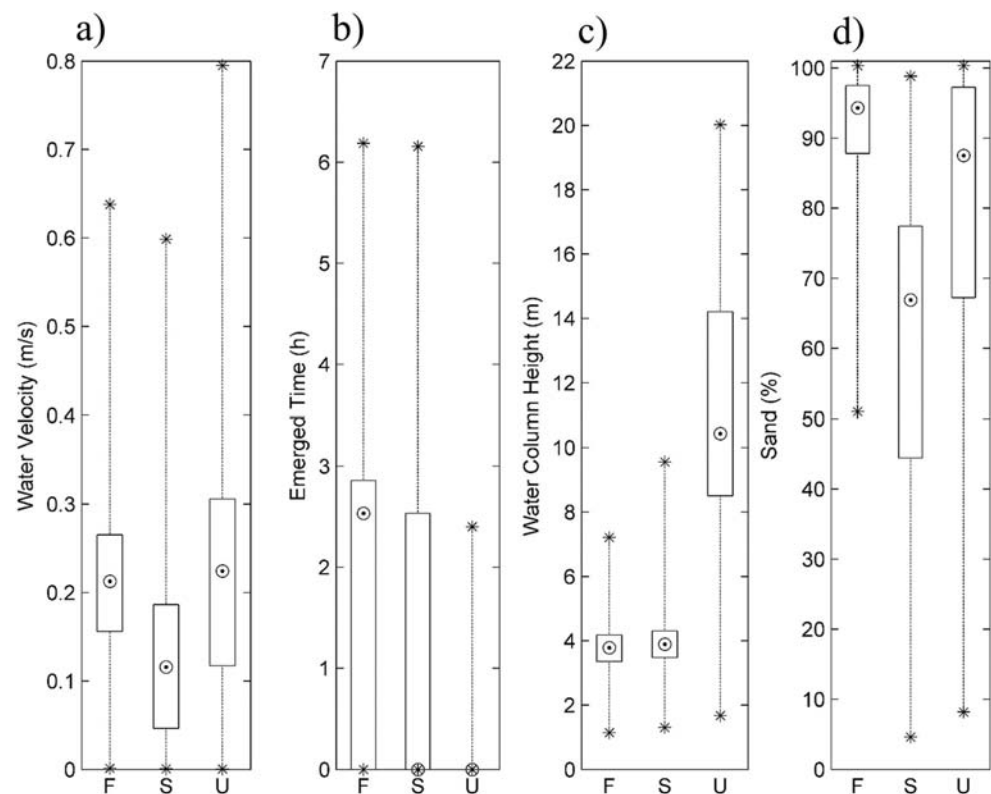
Table 2 Confusion matrix (area, %) for two-classes of field distribution (absence and presence) and three-classes of modelled conditions (unfavourable, stressful, favourable) of *Zostera noltei* in the Bay of Santander (year 2012)

	Predicted habitat conditions		
	Unfavourable	Stressful	Favourable
Field distribution			
Absence	93%	53%	24%
Presence	7%	47%	76%

Vulnerability of *Zostera noltei* to Sea Level Rise

Habitat suitability for *Z. noltei* will vary both spatially and temporally, mainly in deeper areas, where moderate rising levels will reduce the availability of suitable habitats, at an increasing rate from the mid to long term (Fig. 5). The areas with a favourable suitability for the species will be gradually reduced from 2012 to 2100, even more rapidly in the high-end scenario (H++). In this scenario, favourable conditions in deep meadows will turn unfavourable and meadows are expected to be completely lost.

Fig. 5 Suitability maps of *Zostera noltei* (favourable, stressful and unfavourable conditions) in the Bay of Santander for projected GMSL: **a** sea level rise by the year 2065 for the RCP2.6 (0.24 m); **b** SLR by the year 2065 for the RCP8.5 (0.3 m); **c** SLR by the year 2100 for the RCP2.6 (0.4 m); **d** SLR by the year 2100 for the RCP8.5 (0.63 m); **e** SLR by the year 2100 for the H++ (2 m)
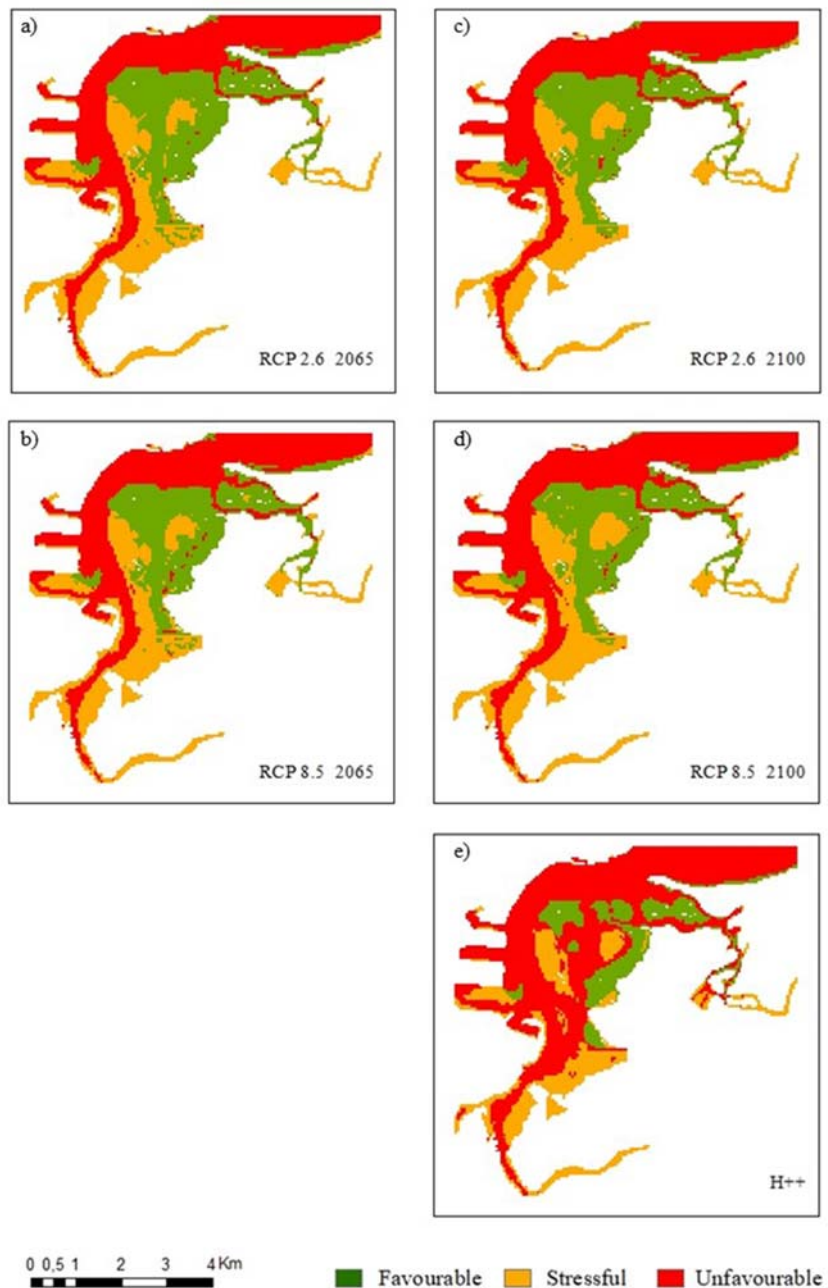
Meadows vulnerability was estimated as the variation in areas with favourable conditions for *Z. noltei* (Fig.6) between the projected maps and the reference year (594.8 ha). Favourable conditions will increase from 3.0 to 3.2% (2065 projections) and from 3.6 to 1.9% (2100 projections) (Table 3) and losses are predicted to range from 8.6 to 10.6 % (2065 projections) and from 11.7 to 52.9% (2100 projections). However, the net balance between gains and losses is negative for all scenarios and projections (Table 3). The availability of favourable habitats will be reduced and more severe in the long term. A rising level of 0.63 m by 2100 will result in a 14.2 % reduction of suitable habitats (IRC=0.2), while 51 % of the meadows will be lost after a 2 m rise (IRC=0.54). In the mid-term, reduction of favourable suitable habitats will range

between 5.6 and 7.3% (IRC 0.11 and 0.13, respectively). The main reductions will occur in the deepest tidal flats and upper flats and certain locations in the low part of the Miera River will gain favourable suitable conditions.

Discussion

The present work deals with how sea level rise translates into changes in seagrass distribution at local scale and how to supply reliable information and tools to predict the vulnerability of shallow coastal ecosystems to the effects of sea level rise.

Fig. 6 Vulnerability of *Zostera noltei* in the Bay of Santander for projected GMSL from 2065 to 2100 expressed through the IRC (gain, loss and no change). **a** Sea level rise at 2065 in the RCP2.6 (0.24 m); **b** SLR at 2065 in the RCP8.5 (0.3 m); **c** SLR at the 2100 in the RCP2.6 (0.4 m); **d** SLR at the 2100 in the RCP8.5 (0.63 m); **e** SLR at the 2100 in the H++ (2 m)
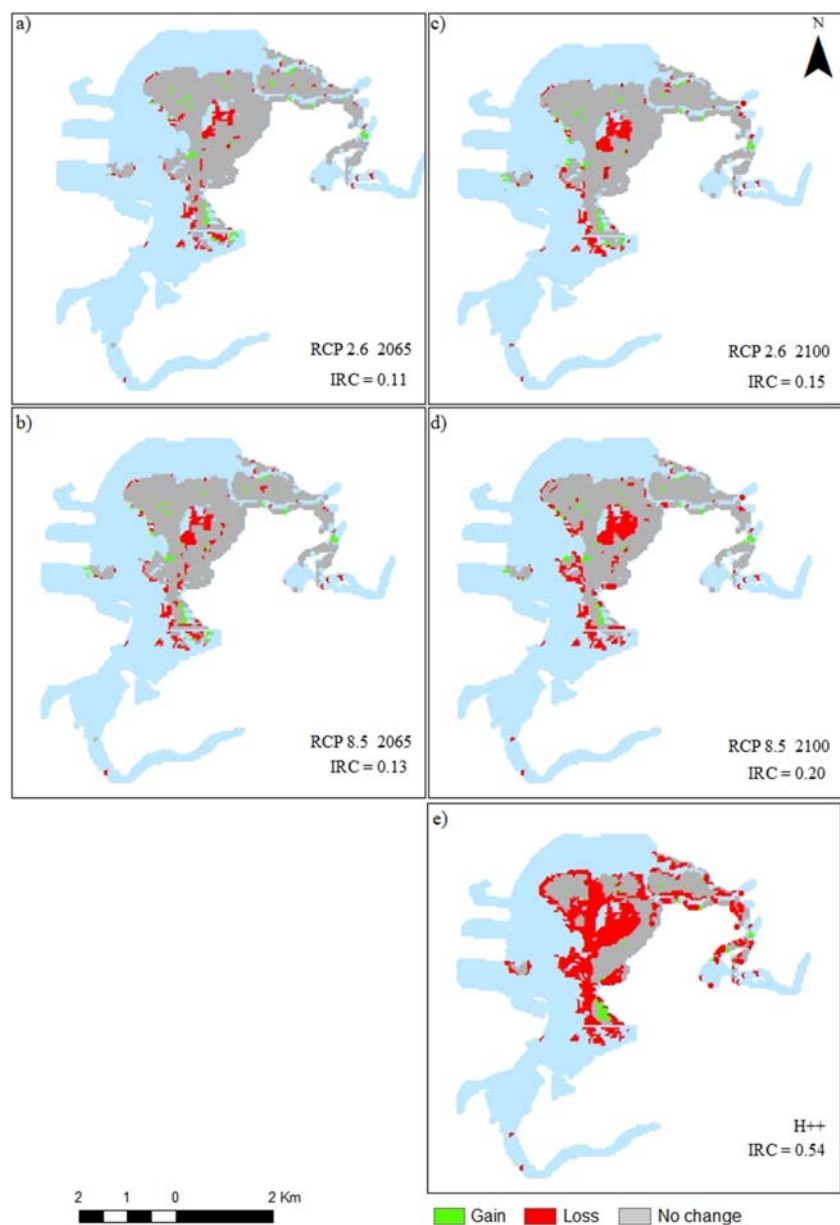
Table 3 Projected changes in favourable habitat suitability for *Zostera noltei* by 2065 (RCP 2.6, 0.24 m and RCP8.5, 0.3 m) and by 2100 (RCP2.6, 0.4 m; RCP8.5, 0.63 m and H++, 2 m)

	Total		Loss		Gain		Balance	
Year 2065								
0.24 m	561.2 ha	94.3%	51.4 ha	8.6%	17.9 ha	3.0%	− 33.5 ha	5.6%
0.3 m	550.8 ha	92.6%	63.2 ha	10.6%	19.2 ha	3.2%	− 43.9 ha	7.3%
Year 2100.								
0.4 m	546.9 ha	91.9%	69.7 ha	11.7%	21.8 ha	3.6%	− 47.8 ha	8.0%
0.63 m	509.7 ha	85.7%	102.7 ha	17.2%	17.6 ha	2.9%	− 85.1 ha	14.2%
2.0 m	291.3 ha	48.9%	315.2 ha	52.9%	11.7 ha	1.9%	− 303.5 ha	51.0%

Total suitable habitat, suitable habitat gain and loss and net balance are indicated for each scenario

Impact of Sea Level Rise on Seagrasses

Eelgrass meadows and the ecosystems they support are threatened by a multitude of environmental factors that are currently changing, or will change in the future (Björk et al. 2008). One of the potential threats from climate change is rising sea levels, the effects of which are now beginning to be detected in seagrass ecosystems (Short et al. 2016). Increasing evidence indicates that the main impact will occur on the deep coastal edge of the meadows, where light availability is minimal and rising sea levels will cause it to reach values that are limiting to seagrass growth. This could result in a complete loss of seagrasses at the deeper edge, while in shallow meadows, biomass and growth are likely to be reduced (Waycott et al. 2007).

The impact will largely depend on the magnitude and speed of sea level rise. Most studies conduct projections of global mean sea level rise (GMSL) based on observations, paleoclimatic analyses and simulations of the climate system (IPCC 2013). Additionally, some authors contemplate another extreme scenario entailing a sea level rise of 2.0 m (Rahmstorf 2007; Pfeffer et al. 2008). This scenario, calculated combining the thermal expansion and all eustatic sources at high, but reasonable values, responds to new concerns about the stability and melting of Greenland's and the West Antarctic's ice sheets. Although the probability of this pessimistic scenario is low, Pfeffer et al. (2008) found it likely to occur under physically possible glaciological conditions, if all variables were quickly accelerated to extremely high limits. In the Bay of Santander, apart from the GMSL, the extreme long-term scenario of 2.0 m (H++) was also simulated. The results are sound enough to allow asserting that sea level rise will highly affect seagrass meadows in the Bay of Santander. Predictions from the model indicate that the distribution of *Z. noltei* will experience considerable spatial and temporal variations, mainly in deeper areas, where moderate rising levels will reduce the availability of suitable habitats, at an increasing rate in the mid to long term. A rising level of 0.63 m by 2100 will result in a 14.2% reduction in suitable habitats, while a 51% loss will

occur with a sea rise of 2 m. Our results differ from those found by Valle et al. (2014) and Chust et al. (2011) in the Oka estuary, also located in the Bay of Biscay. For a 0.49 m sea level rise at the end of the century, Valle et al. (2014) predicted an increasing of suitable intertidal habitat of 14–18% and Chust et al. (2011) a shoreline retreat between 25 and 40% of their width. For the same scenario, we estimated an 8% reduction in suitable habitats in the Bay of Santander. These deviations can be explained by differences in the variables and models considered and by the different estuaries' dynamics. At these spatial scales, the responses of coastal ecosystems depend on local hydrogeomorphological processes and local rates of sea level rise. Therefore, faced with the same threat, the same community may show different responses in different estuaries and even in the same one.

Adaptation of Seagrasses to Sea Level Rise

The projected loss of suitable habitats in the Bay of Santander in the mid and long terms will be partly offset by a net gain, although the total balance will remain negative. Losses at the deep edge of seagrass meadows might be compensated by shoreward migrations or intrusions higher up into estuaries and rivers (Björk et al. 2008; Short et al. 2016). Areas having extensive shallow mudflats will provide an opportunity for seagrass meadow expansion, although this colonization is often prevented by anthropogenic alterations to shorelines (Short et al. 2016; Short and Neckles 1999). Shoreward movements are restricted by estuary hypsometry and, particularly, by land elevation with respect to sea level. This factor controls the ratio between lost and gained areas by seagrasses, as well as the rate at which new submerged areas can be colonized (Davis et al. 2016; Waycott et al. 2007). In the Bay of Santander, the hypsometric curve is mainly convex. This means that the area around the estuary is anthropized, the accommodation space is reduced and thereby conditions in which seagrasses could migrate shoreward are limited.

However, the southern Bay still has extensive natural areas, where seagrasses may move shoreward.

Another important aspect allowing adaptation to rising sea levels in shallow areas is the capacity of vegetated coastal habitats to raise the sea floor at speeds that can match or exceed current sea level rise, thereby counterbalancing the effect of sea level rise (Duarte et al. 2013). The effectiveness of sediment accretion by vegetated coastal habitats as an adaptation to sea level rise is dependent on the rates of accretion and local processes such as compaction, subsidence and rates of sea level rise (Duarte et al. 2013). However, predicting sediment accretion is complicated by the many interacting factors affecting the meadows (Aoki et al. 2020). For example, concurrently with sea level rise, seagrass canopies attenuate energy and slow currents, leading to enhanced accretion rates, while the roots and rhizomes stabilize sediments (Aoki et al. 2020). These self-amplifying mechanisms may be critical to seagrass adaptation (Maxwell et al. 2016). The accretion rate in the Bay of Santander is estimated at 0.35 cm year^{-1} (Gelen et al. 2004), the mean annual maximum shoot density is 3357.14 shoots m^{-2} (Ondiviela et al. 2018) and the area occupied by *Z. noltei* has increased continuously over the last 20 years (Calleja et al. 2017). These trends suggest that current feedbacks are positively modifying the structure and functioning of seagrass ecosystems and that current environmental conditions in the Bay of Santander allow meadows to be self-controlled. Consequently, in the near future, seagrass accretion can be expected to be sufficient to mitigate the direct effects of sea level rise on its depth distribution (Aoki et al. 2020). On the contrary, long-term accretion rates will likely be lower, due to compaction of deep sediments, variations in the sediment supplied by the river basin or increases in the erosion rates due to intensifying river flows (Santos et al. 2012). Under this situation, elevation rates for vegetated coastal habitats could be lower than accretion rates and meadows may show a net subsidence (Duarte et al. 2013).

When considering the adaptation and vulnerability of small fast-growing seagrass species, it is accepted that dense and non-fragmented meadows in healthy environments, with good trophic interactions, are less vulnerable. Indeed, seagrasses are capable of seed production and dispersal (Waycott et al. 2007). Inappropriate coastal sediments, rocky shores or other barriers will likely limit the colonization capacity of seagrasses, but species with rapid recruitment capabilities (i.e. *Zostera noltei*) will occupy new areas more rapidly than slower recruiting species (Waycott et al. 2007). The main adaptive advantages of eelgrasses in the Bay of Santander are their natural traits to tolerate the high variability in environmental conditions (Calleja et al. 2017; Ondiviela et al. 2018). As shown by various authors, the larger the trait-variability, the more likely the system's survival during periods of stress (Ehlers et al. 2008; Maxwell et al. 2016; O'Brien et al. 2018).

Hypotheses, Surrogates, Assumptions and Uncertainties

The success in predicting vegetation patterning is linked to the strength of the explanatory variables selected. Seagrass ecosystems are stochastic environments where functions, ecological processes and stressors operate simultaneously and at different spatial and time scales (Greve and Binzer 2004). An important hypothesis supporting the selection of variables in this work is that climate conditions govern local hydrodynamics, which in turn play a relevant role in vegetation distribution. The expected effects of sea level rise will be to increase water depths, change tidal variation, change currents, and increase turbidity and seawater intrusion into estuaries and rivers (Short and Neckles 1999). Accordingly, the explanatory variables used to predict the habitat suitability of *Z. noltei* in the Bay of Santander are those directly affected by sea level rise. The approach developed simplifies the complex dynamics and relationships occurring in natural environments (biology responses, seagrass ecology, etc.), through a set of surrogates, hypotheses and assumptions. These simplifications include the description of natural systems by a reduced number of variables, selected to reproduce suitable habitats for *Z. noltei*, as well as the changes caused by sea level rise. Currents and substratum are known to play an important role in creating niches for submerged aquatic vegetation and main factors controlling seagrass settlement (Koch 2001); water column height is used as a proxy for light availability; and ultimately the competition interactions between *Z. noltei* and *Z. marina* are considered through variations in the depth distribution limit between both species, which is estimated as emerged time. Although in some locations both species coexist, forming mixed meadows, competition between both seagrasses sets clear limits to their distribution (Marbà et al. 2004).

A main assumption in the model applied is the absence of changes in sediment dynamics, and thereby in bathymetry and sediment characteristics. We are aware that this is a strong limitation in our approach, but modelling sediment changes and bathymetry in mid- and long-term projections causes enormous uncertainty. Different approaches for modelling sediment dynamics (e.g. MOHID, DELFT 3D) are found in the literature, but their applicability in long-term predictions is still under debate (Coco et al. 2013), since, apart from computing issues, they can significantly increase the difficulty implied in isolating and interpreting driving feedback. For instance, non-linear effects (e.g. small numerical instabilities, effect of different sediment transport formulas and timing of marine dynamics events), which are not obvious at short time scales, may grow significantly and prevail in the long term, rendering unrealistic solutions. Additionally, the characterization of the Miera River would be another weakness, since long-term sediment yields will depend on the socioeconomic

Fig. 7 Changes in velocity regime and water column height between 2012 and the conditions modelled for a 0.63 m sea level rise (projection 2100). Positive values indicate that the velocity and the water column height have increased since 2012. Formula applied: reference condition (2012)–sea level rise condition (RCP8.5-2100)
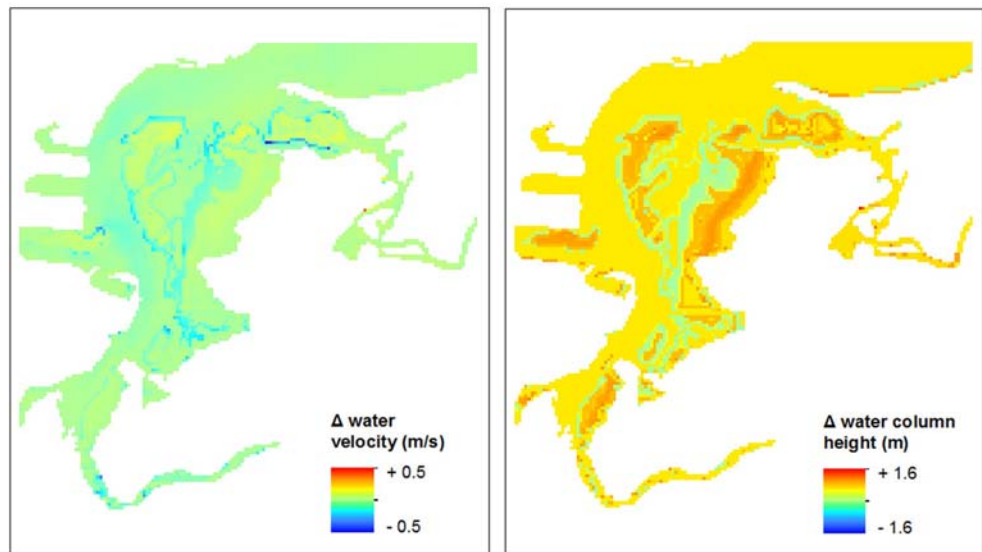
evolution of the river basin, introducing further uncertainties into the model, and making it highly inaccurate. The sum of these uncertainties led us to omit morphodynamics modelling from our approach. However, to illustrate possible variations in the estuary's morphodynamics, Fig. 7 shows changes in the velocity regime and water column height from 2012 to 2100 (RCP 8.5). The simulation highlights variations in the confluence between the Miera River and the estuary, which could trigger changes in the accretion and erosion rates as well as in the Bay's morphodynamics. These changes in sediment dynamics could lead to higher losses of *Z. noltei* than those projected in Fig. 6 for the same scenario. But as noted before, these results should also consider processes such as compaction and subsidence.

Vulnerability of Seagrasses to Sea Level Rise

In this study, vulnerability to sea level rise is understood as variations in the distribution and abundance of favourable habitats for *Z. noltei* between projected maps and a given reference year. This definition differs from other previous ones (e.g. Chust et al. 2013; Halpern et al. 2007), but is consistent with the purpose of this study, which seeks to evaluate the balance between gain and loss of suitable habitats for the species.

As discussed throughout the previous sections, successfully predicting seagrass responses to sea level rise is subject to numerous uncertainties related with the hypotheses, assumptions and models applied, but also with the feedbacks and self-amplifying mechanisms that take place in shallow coastal ecosystems. According to our projections, *Z. noltei* meadows in the Bay of Santander are highly vulnerable to sea level rise and in the mid and long terms, large areas of seagrasses will be lost. However, the revision of the main factors regulating

seagrass adaptation allows to be confident regarding the adaptation capacity of eelgrass *Z. noltei* in the near future.

Conclusions

To evaluate mid and long-term changes in the habitat suitability of *Zostera noltei* a combination of clustering techniques – Self organizing maps and K-means-, considering RCP and high-end projections, is used. The study, developed at the Bay of Santander, provides evidence indicating that sea level rise will highly affect meadows of *Zostera noltei*. This species will experience an important spatial variability, mainly in deeper areas, where moderate rising levels will substantially reduce the availability of suitable habitats for this species. This process will intensify over time and seagrass meadows are expected to be severely affected in the long term, especially in the absence of major changes to sediment dynamics. A rising level of 0.63 m by 2100 will result in a 14.2 % reduction in suitable habitats, while a 51 % loss will occur with a sea level rise of 2 m. However, the observed resilience and increasing trends in the last two decades, the current accretion rates and the availability of shallow natural mudflats where seagrasses can migrate to, allows us to be confident about *Zostera noltei's* capacity to adapt to changing conditions in the near future. Success in the prediction of seagrass responses to sea level rise is subject to numerous uncertainties related with the hypotheses, assumptions and models applied and with the feedbacks and self-amplifying mechanisms taking place in shallow coastal ecosystems. However, from our study, it can be stated that the clustering approach is a useful tool to understand changes caused by sea level rise on seagrasses, with two main strengths: it is locally applicable and can be transferred to any shallow coastal ecosystem (e.g.

marsh vegetation), or driver (e.g. warming, sediment transport).

References

Aoki, L.R., McGlathery, K.J., Wiberg, P.L., Al-Haj, A. 2020. Depth affects seagrass restoration success and resilience to marine heat wave disturbance. Estuaries and Coasts. https://doi.org/10.1007/s12237-019-00685-0. In Press, 43, 2, 316, 328.

Björk, M., F. Short, E. Mcleod, and S. Beer, eds. 2008. *Managing seagrasses for resilience to climate change*, 56. Gland: IUCN.

Calleja, F. 2019. Spatial and temporal distribution of the vegetation in tidal estuaries: Interactions between native and invasive species. *PhD Thesis*. University of Cantabria.

Calleja, F., C. Galván, A. Silió-Calzada, J.A. Juanes, and B. Ondiviela. 2017. Long-term analysis of *Zostera noltei*: A retrospective approach for understanding seagrasses' dynamics. *Marine Environmental Research* 130: 93–105.

Camus, P., F.J. Mendez, R. Medina, and A.S. Cofiño. 2011. Analysis of clustering and selection algorithms for the study of multivariate wave climate. *Coastal Engineering* 58: 453–462.

Céréghino, R., F. Santoul, A. Compin, and S. Mastrorillo. 2005. Using self-organizing maps to investigate spatial patterns of non-native species. *Biological Conservation* 125: 459–465.

Charpentier, A., P. Grillas, F. Lescuyer, E. Coulet, and I. Auby. 2005. Spatio-temporal dynamics of a *Zostera noltii* dominated community over a period of fluctuating salinity in a shallow lagoon, Southern France. *Estuarine, Coastal and Shelf Science* 64 (2–3): 307–315.

Chust, G., Á. Borja, A. Caballero, X. Irigoien, J. Sáenz, R. Moncho, M. Marcos, P. Liria, J. Hidalgo, M. Valle, and V. Valencia. 2011. Climate change impacts on coastal and pelagic environments in the southeastern Bay of Biscay. *Climate Research* 48: 307–332.

Chust, G., A. Albaina, A. Aranburu, Á. Borja, O.E. Diekmann, A. Estonba, J. Franco, J.M. Garmendia, M. Iriondo, I. Muxika, F. Rendo, J.G. Rodríguez, O. Ruiz-Larrañaga, E.A. Serrão, and M. Valle. 2013. Connectivity, neutral theories and the assessment of species vulnerability to global change in temperate estuaries. *Estuarine, Coastal and Shelf Science* 131: 52–63.

Coco, G., Z. Zhou, B. van Maanen, M. Olabarrieta, R. Tinoco, and I. Townend. 2013. Morphodynamics of tidal networks: Advances and challenges. *Marine Geology* 346: 1–16.

Cohen, J. 1960. A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* 20 (1): 37–46.

Davis, T., D. Harasti, S. Smith, and B. Kelaher. 2016. Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments. *Estuarine, Coastal and Shelf Science* 181: 294–301.

de la Hoz, C.F., E. Ramos, A. Puente, F. Méndez, M. Menéndez, J.A. Juanes, and Í.J. Losada. 2018. Ecological typologies of large areas. An application in the Mediterranean Sea. *Journal of Environmental Management* 205: 59–72.

De la Hoz, C.F., E. Ramos, A. Puente, F. Mendez, M. Menendez, J.A. Juanes, and I.J. Losada. 2017. Ecological typologies of large areas. An application in the Mediterranean Sea. *Journal of Environmental Management* 205: 59–72.

Duarte, C.M., Í.J. Losada, I.E. Hendriks, I. Mazarrasa, and N. Marbà. 2013. The role of coastal plant communities change mitigation and adaptation. *Nature Climate Change* 3: 961–968.

Ehlers, A., B. Worm, and T.B. Reusch. 2008. Importance of genetic diversity in eelgrass Zostera marina for its resilience to global warming. *Marine Ecology Progress Series* 355: 1–7.

De los Santos, C.B., D. Krause-Jensen, T. Alcoverro, N. Marbà, C.M. Duarte, M.M. van Katwijk, M. Pérez, J. Romero, J.L. Sánchez-Lizaso, G. Roca, E. Jankowska, J.L. Pérez-Lloréns, J. Fournier, M. Montefalcone, G. Pergent, J.M. Ruiz, S. Cabaço, K. Cook, R.J. Wilkes, F.E. Moy, G.M.-R. Trayter, X.S. Arañó, D.J. de Jong, Y. Fernández-Torquemada, I. Auby, J.J. Vergara, and R. Santos. 2019. Recent trend reversal for declining European seagrass meadows. *Nature Communications* 10: 3356.

Fournier, A., M. Barbet-Massin, Q. Rome, and F. Courchamp. 2017. Predicting species distribution combining multi-scale drivers. *Global Ecology and Conservation* 12 (November): 215–226. https://doi.org/10.1016/j.gecco.2017.11.002.

Felicísimo, Á. M. (coord.) 2011. *Impactos, vulnerabilidad y adaptación al cambio climático de la biodiversidad española. 2. Flora y vegetación.* Oficina Española de Cambio Climático, Ministerio de Medio Ambiente y Medio Rural y Marino. Madrid, 552 pp.

Frau, D., B. Ondiviela, C. Galván, and J.A. Juanes. 2014. The role of the hydrodynamic regime in the distribution of the invasive shrub *Baccharis halimifolia* (Compositae) in Oyambre Estuary (Cantabria, Spain). *Limnetica* 33 (1): 1–12.

Frederiksen, M., D. Krause-Jensen, M. Holmer, and J.S. Laursen. 2004. Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: Influence of physical setting. *Aquatic Botany* 78: 147–165.

Galván, C., J.A. Juanes, and A. Puente. 2010. Ecological classification of European transitional waters in the North-East Atlantic eco-region. *Estuarine, Coastal and Shelf Science* 87 (3): 442–450.

Gelen, A., J. Soto, J. Gómez-Arozamena, O. Díaz. 2004. Sediment dating of Santander Bay, Spain. Journal of Radioanalytical and Nuclear Chemistry 261(2):437–441.DOI: https://doi.org/10.1023/B:JRNC.0000034882.14464.7f

Guisan, A., Thuiller, W., & Zimmermann, N. E. 2017. Habitat suitability and distribution models. doi: https://doi.org/10.1017/9781139028271.

Greve, T.M. and Binzer, T., 2004. Which factors regulate seagrass growth and distribution? In: J. Borum, C.M. Duarte, D. Krause-Jensen and T.M. Greve (Editors), *European seagrasses: an introduction to monitoring and management. The M&MS proje*ct. Monitoring and Managing of European Seagrasses EVK3-CT-2000-00044, pp. 19-23.

Halpern B.S., K.A. Selkoe, F. Micheli, C.V. Kappel. 2007. Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats. *Conservation Biology* 21 (5):1301–1315

Hopton, M.E., and A.L. Mayer. 2006. Using self-organizing maps to explore patterns in species richness and protection. *Biodiversity and Conservation* 15: 4477–4494.

IPCC, 2013. Summary for policymakers. In: *Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jiménez, M., S. Castanedo, R. Medina, and P. Camus. 2012. A methodology for the classification of estuary restoration areas: A management tool. *Ocean & Coastal Management* 69: 231–242.

Kairis, Peter A. & Rybczyk, John M., 2010. "Sea level rise and eelgrass (*Zostera marina*) production: A spatially explicit relative elevation model for Padilla Bay, WA, *Ecological Modelling*, Elsevier, vol. 221(7), pages 1005–1016.

Koch, E. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24 (1): 1–17.

Marbà, N., Duarte, C.M., Alexandre, A. and Cabaço, S., 2004. How do seagrasses grow and spread? In: J. Borum, C.M. Duarte, D. Krause-Jensen and T.M. Greve (Editors), *European seagrasses: an introduction to monitoring and management. The M&MS project. Monitoring and Managing of European Seagrasses* EVK3-CT-2000-00044, pp. 11-18.

Maxwell, P.S., J.S. Eklöf, M.M. Van Katwijk, K.R. O'Brien, M. De la Torre-Castro, C. Boström, T.J. Bouma, D. Krause-Jensen, R.K.F. Unsworth, B.I. Van Tussenbroek, and T. Van der Heide. 2016. The fundamental role of ecological feedback mechanisms in seagrass ecosystems—A review. *Biological Reviews*. https://doi.org/10.1111/brv.12294.

Mele, P.M., and D.E. Crowley. 2008. Application of self-organizing maps for assessing soil biological quality. *Agriculture, Ecosystems & Environment* 126: 139–152.

Monsreud, R.A., and R. Leemans. 1992. Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling* 62: 275–293.

Nicholls, R.J., and A. Cazenave. 2010. Sea-level rise and its impact on coastal zones. *Science* 328 (5985): 1517–1520.

O'Brien, K.R., Waycott, M., Maxwell,P., Kendrick, G.A.,Udy, J.W., Ferguson, A.J.P.,Kilminster, K., Scanes, P., McKenzie, L.J., McMahon, K., Adams, M.P., Samper-Villarreal, J., Collier, C., Mitchell Lyons, M., Mumby, P.J., Radke, L., Christianen, M. J.A. Dennison, W.C. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Marine Pollution Bulletin 134: 166–176.

Ohlson, T., V. Aggarwal, A. Elofsson, and R. MacCallum. 2006. Improved alignment quality by combining evolutionary information, predicted secondary structure and self-organizing maps. *BMC Bioinformatics* 7 (1): 357.

Ondiviela, B., I.J. Losada, J.L. Lara, M. Maza, C. Galván, T.J. Bouma, and J. van Belzen. 2014. The role of seagrasses in coastal protection in a changing climate. *Coastal Engineering* 87 (158): 168.

Ondiviela, B., M. Recio, and J.A. Juanes. 2015. A management approach for the ecological integrity of NE Atlantic estuaries. *Ecological Indicators* 52: 105–115.

Ondiviela, B., L. Fernández, A. Puente, G. García-Castrillo, and J.A. Juanes. 2018. Characterization of a resilient seagrass meadow during a decline period. *Scientia Marina* 82 (1). https://doi.org/10.3989/scimar.04616.18A.

Pfeffer, W.T., J.T. Harper, and S. O'Neel. 2008. Kinematic constraints on glacier contributions to 21st-century sea-level rise. *Science* 321 (5894): 1340–1343.

Rahmstorf, S. 2007. A semi-empirical approach to projecting future sea-level rise. *Science* 315 (5810): 368–370.

Russo, T., M. Scardi, and S. Cataudella. 2014. Applications of self-organizing maps for ecomorphological investigations through early ontogeny of fish. *PLoS One* 9 (1). https://doi.org/10.1371/journal.pone.0086646.

Santos, I.R., B.D. Eyre, and M. Huettel. 2012. The driving forces of porewater and groundwater flow in permeable coastal sediments: A review. *Estuarine, Coastal and Shelf Science* 98: 1–15.

Shaughnessy, F.J., W. Gilkerson, J.M. Black, D.H. Ward, and M. Petrie. 2012. Predicted eelgrass response to sea level rise and its availability to foraging Black Brant in Pacific coast estuaries. *Ecological Applications* 22 (6): 1743–1761.

Solidoro, C., V. Bandelj, P. Barbieri, G. Cossarini, and S.F. Umani. 2007. Understanding dynamic of biogeochemical properties in the northern Adriatic Sea by using self-organizing maps and K-means clustering. *Journal of Geophysical Research* 112: C07S90.

Spalding, M.D., S. Ruffo, C. Lacambra, I. Meliane, L.Z. Hale, C.C. Shepard, and M.W. Beck. 2014. The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. *Ocean and Coastal Management* 90: 50–57.

Short, F.T., and H.A. Neckles. 1999. Review. The effects of global climate change on seagrasses. *Aquatic Botany* 63: 169–196.

Short, F.T., S. Kosten, P.A. Morgan, S. Malone, and G.E. Moore. 2016. Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany* 135: 3–17.

Toimil, A., I.J. Losada, P. Camus, and P. Diaz-Simal. 2017. Managing coastal erosion under climate change at the regional scale. *Coastal Engineering* 128: 106–122.

Traboni, C., S.D. Mammola, M. Ruocco, Y. Ontoria, J.M. Ruiz, G. Procaccini, and L. Marín-Guirao. 2018. Investigating cellular stress response to heat stress in the seagrass *Posidonia oceanica* in a global change scenario. *Marine Environmental Research* 141: 12–23.

Valle, M., G. Chust, A. del Campo, M.S. Wisz, S.M. Olsen, J.M. Garmendia, and A. Borja. 2014. Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise. *Biological Conservation* 170: 74–85.

Waycott, M., C. Collier, K. Mcmahon, P. Ralph, L. McKenzie, J. Udy, and A. Grech. 2007. Vulnerability of seagrasses in the Great Barrier Reef to climate change. In *Climate change and the Great Barrier Reef: A vulnerability assessment*, ed. Great Barrier Reef Marine Park Authority. Townsville: Great Barrier Reef Marine Park Authority.

Weber, M., H. Teeling, S.X. Huang, J. Waldmann, M. Kassabgy, B.M. Fuchs, A. Klindworth, C. Klockow, A. Wichels, G. Gerdts, R. Amann, and F.O. Glockner. 2011. Practical application of self-organizing maps to interrelate biodiversity and functional data in NGS-based metagenomics. *ISME Journal* 5 (5): 918–928.