Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise

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A B S T R A C T

In future decades, coastal ecosystems are expected to be exposed to increased risk of experiencing adverse consequences related to climate change, exacerbated by human induced pressures. The seagrass *Zostera noltii* forms meadows mainly within the intertidal zone, leading it to be particularly vulnerable to seawater temperature increase and sea level rise (SLR). Considering the presently declining situation and the predicted scenarios of increasing seawater temperature and SLR by the end of the 21st century, we assessed the response of *Z. noltii* to climate change (i) accounting for changes in seawater temperature at its entire biogeographical range level; and (ii) under SLR scenarios at estuary level (Oka estuary, Basque Country, south-eastern Bay of Biscay). Objectives were addressed coupling habitat suitability models with climate change simulations. By the end of the 21st century, seawater temperature increase will trigger a northward distributional shift of 888 km in the suitable habitat of the species, and a retreat of southernmost populations. The loss of southernmost populations due to climate change may imply future conservation problems. In contrast, SLR and derived changes in current velocities are expected to induce the landward migration of the species in the Oka estuary, increasing the available suitable intertidal areas (14–18%) to limits imposed by anthropogenic barriers. This modelling approach could lead to an advanced understanding of the species' response to climate change effects; moreover, the information generated might support conservation actions towards the sites where the habitat would remain suitable for the species under climate change.

1. Introduction

Recent climate change has impacted marine environments with documented effects on the phenology of organisms, the range and distribution of species, and the composition and dynamics of communities (Philippart et al., 2011; Richardson et al., 2012). In future decades, coastal ecosystems are expected to be exposed to increased risk of experiencing adverse consequences related to climate change, exacerbated by increasing human induced pressures (Nicholls et al., 2007). Thus, understanding the response of coastal ecosystems to climate change has become an urgent challenge (Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010). Seagrasses are marine flowering plants that form one of the richest and most important coastal habitats (Short et al., 2011). They play key roles in ecosystem functioning (Duarte, 2002) supporting a range of keystone and ecologically important marine species from

all trophic levels (Orth et al., 2006), which lead them to provide numerous important ecological services to the marine environment (Duarte et al., 2008). Their value is recognised by the Convention on Biological Diversity (1992) and the seagrass meadow area is considered a priority habitat under the European Commission Habitats Directive (92/43/EEC). Moreover, according to the European Water Framework Directive (2000/60/EC), these angiosperms have been listed as one of the five biological quality elements to be included in the ecological quality assessment in marine waters (Marbà et al., 2013). Favoured by this legislation framework, seagrass habitats are nowadays specifically targeted for conservation and restoration (Green and Short, 2003). However, over the last two decades, up to 18% of the documented seagrass area has been lost (Green and Short, 2003), with rates of decline accelerating in recent years (Waycott et al., 2009). This present situation of declining seagrasses may be exacerbated by additional global change drivers (Short and Neckles, 1999), including global warming (Jordà et al., 2012) and sea level rise (SLR) (Saunders et al., 2013). Moreover, considering the key role of seagrasses in the ecosystem

function, such decline might be detrimental to those species that depend on them, including economically important fishes and invertebrates (Hughes et al., 2009).

Zostera noltii is widely distributed along the coasts of the Atlantic Ocean (Green and Short, 2003), from the south of Norway to the south of the Mauritanian coast, being also present in the Mediterranean, Black, Azov, Caspian, Aral Seas (Moore and Short, 2006) and the Canary Islands (Diekmann et al., 2010) (Fig. 1a). It is listed in the Least Concern category of the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species, primarily due to its large range size, but it has declining population trends (Short et al., 2010) and is therefore in need of protection and monitoring. This seagrass species forms meadows mainly within the intertidal zone, i.e. the interface between marine and terrestrial environments (Moore and Short, 2006), leading it to be particularly vulnerable to climate change derived effects, such as increasing temperature and SLR (Chust et al., 2011; Massa et al., 2009; Short and Neckles, 1999); and to anthropogenic pressures (Duarte et al., 2008). Global mean upper ocean temperatures have increased over decadal times scales from 1971 to 2010, with a global average warming trend of 0.11 °C per decade in the upper 75 m of the ocean (IPCC, 2013). The global ocean is predicted to continue warming during the 21st century (Collins et al., 2012) and it is very likely that, by the end of the century, over about 95% of the world ocean, regional SLR will be positive (Church et al., 2011).

Considering the scenarios of increasing seawater temperature and SLR by the end of the 21st century, the objectives of this study were: (i) to assess the future geographical distribution of the climatic niche for *Z. noltii* meadows at its overall biogeographical range level; and (ii) to assess the response of *Z. noltii* to SLR at local level, using the Oka estuary (south-eastern Bay of Biscay) as a case study. Whilst global warming threat is assessed using global climate models, SLR influence is site specific and must be assessed using regional models. Particularly within the Bay of Biscay, mean sea level has risen over the last decades (Chust et al., 2011, 2009). Moreover, Basque estuaries (in northern Spain) (Fig. 1b) have been radically transformed by anthropogenic activities during the 20th century (Chust et al., 2009), which might produce a joint SLR effect (Chust et al., 2011). In addition, *Z. noltii* has been recently listed as endangered species within this region (Aizpuru et al., 2010).

According to the expected changes in seawater thermal conditions, we first hypothesize that a poleward shift in biogeographical distribution of *Z. noltii* might be likely to occur. Our second hypothesis is that SLR and derived changes in current velocities might redistribute the suitable habitat of the species, depending on the estuarine geomorphology. Modelling present day species habitat relationships and projecting these under future global change scenarios allows the assessment of changes in available habitat (e.g. Mendoza-González et al., 2013; Saunders et al., 2013). Therefore, to address the hypotheses and objectives, habitat suitability
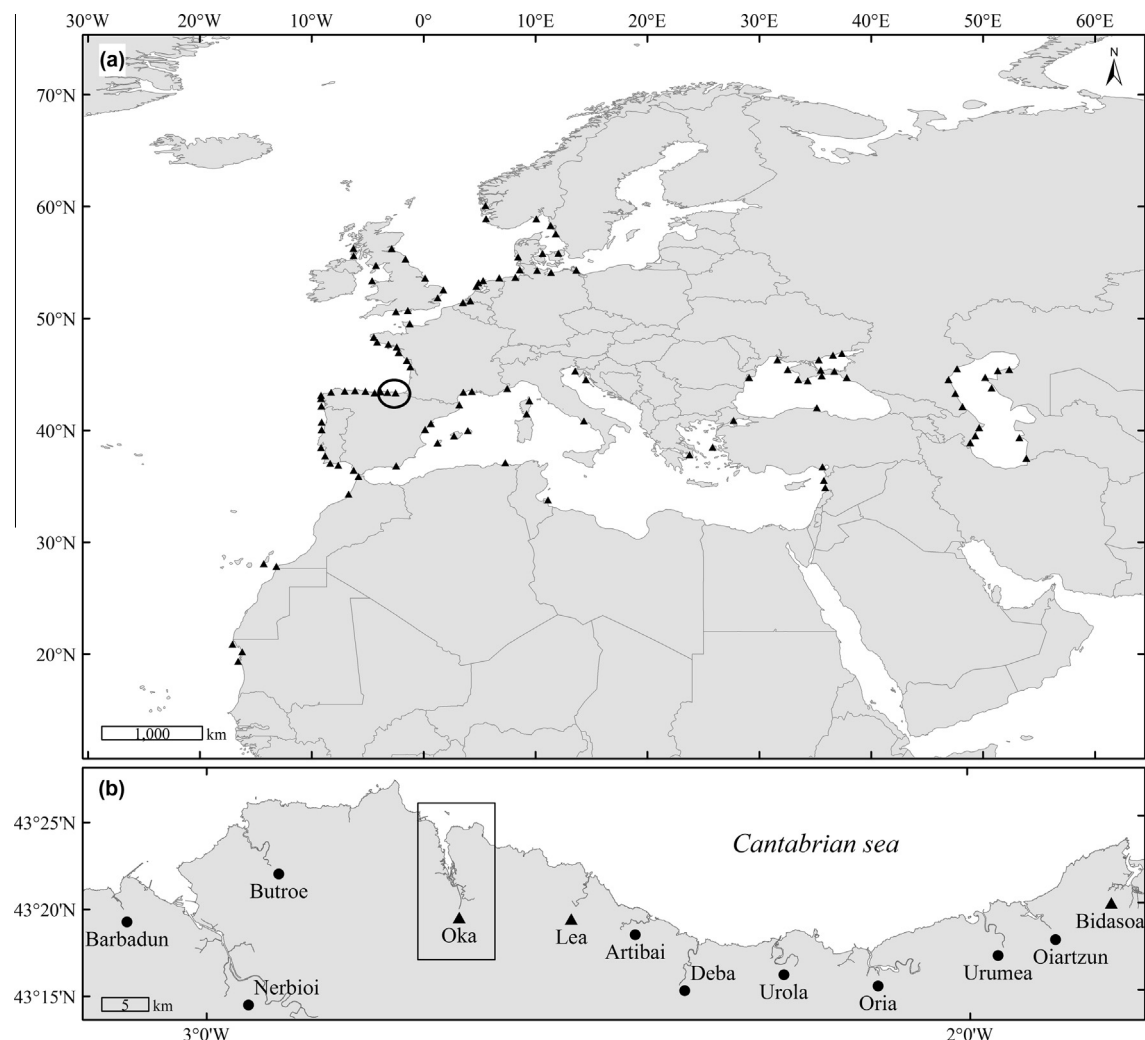

Fig. 1. (a) *Zostera noltii* occurrence records (black triangles) within the entire biogeographical distribution range, circle highlighting the Basque coast; (b) Basque coast estuaries where *Zostera noltii* occurs (black triangles) and where it is not present (round dots), black rectangle highlighting the Oka estuary.

models (e.g. Guisan and Zimmermann, 2000) were coupled with simulations obtained from global warming and regional SLR scenarios.

2. Material and methods

2.1. Data for biogeographical range level analysis

The study area addressing the first objective encompasses the coastal strip of the entire biogeographical distribution of the species (Fig. 1a). The Global Distribution of Seagrasses Dataset (V2.0, 2005), prepared by United Nations Environment Programme World Conservation Monitoring Centre (available at: http://data.unep-wcmc.org/) and used in the creation of the "World Atlas of Seagrasses" (Green and Short, 2003), was sourced from Ocean Data Viewer, a website which provides access to important data for marine and coastal biodiversity conservation. Additional occurrence records of the species were obtained from the Global Biodiversity Information Facility (available at: http://data.gbif.org/welcome.htm), an open access global network of biodiversity data. Compiled distributional data were vetted for locational reliability and the number of observations was reduced locating only one observation within the 1° by 1° cells from the study area. In addition, new occurrences were added along the Iberian Peninsula in accordance to literature (Coyer et al., 2004; Diekmann et al., 2010, 2005; Laborda et al., 1996; Valle et al., 2011). In total, species distribution data accounted for 112 occurrence points (Fig. 1a). A matching number of absence records were generated at the same resolution as presence records along the study area in those sites where the species has never been cited.

Environmental data on seawater surface temperature (SST) was sourced from an Atmosphere–Ocean Coupled General Climate Model (AOGCM) simulation, which was forced under the Representative Concentration Pathway (RCP) 8.5 scenario (Riahi et al., 2011). The RCP 8.5 scenario corresponds to the pathway with the highest greenhouse gas emissions considered in the new Coupled Model Intercomparison Project Phase 5 (CMIP5) projections (Andrews et al., 2012) and is chosen here to span the widest possible range of environmental changes. In this scenario, the global average temperature warming exceeds 4 °C by the end of the 21st century following a gradual signal which is reflected in an approximately linear evolution of ocean properties. Aiming to assess the reliability of these simulations, ocean hindcast simulations based on atmospheric reanalysis were also compiled from the dynamical model NEMO (Nucleus for European Modelling of the Ocean) under the forcing derived from National Centers for Environmental Prediction (NCEP) for the period from 1948 to end of August 2010. A reference period from 2006 to end of August 2010 was fitted in order to validate the simulated values. To this end, averaged value (maximum, minimum, mean and standard deviation) for the reference period (2006 – August 2010) were compared between SST simulated data under RCP 8.5 scenario and NCEP observations. Spatially, RCP 8.5 fitted in well with NCEP for all statistics, with a mean R^2 of 0.92 ± 0.1. To predict the species distribution under present climate, data were also averaged for the period from 2006 to 2020 and same statistics were derived. To project the model to the future conditions, average values were calculated for the period from 2085 to 2100.

2.2. Data for estuary level analysis

The Oka estuary (Fig. 1b), in the south-eastern Bay of Biscay (north of the Iberian Peninsula) was selected as study area to assess the response of the species to SLR. As explained by Monge-Ganuzas et al. (2013), this estuary is a drowned fluvial valley type, meso-macrotidal, with semidiurnal tides (tidal range 4.5 m on springs and 1.5 m on neaps), well-mixed water column and tide dominated. It is one of the most biologically diverse and best conserved estuaries in the Basque Country (Spain). Data on the species distribution within the Oka estuary were obtained from previous studies (Valle et al., 2011) and from a specific field sampling carried out in August 2010 where, besides confirming the data summarised in Valle et al. (2011), new presence and absence locations were acquired with a Trimble R6 GNSS system (differential GPS, with Real Time Kinematic (RTK) technologies). This high precision GPS delivers the accuracy and reliability required for precision surveying with superior tracking and RTK performance, having a maximum horizontal position error of 1.5 cm and a maximum vertical position error of 2 cm.

Environmental variables which are known to affect the *Z. noltii* distribution (Valle et al., 2011) were collected and two environmental predictor data subsets were defined. The first subset included four variables at a very high resolution (1 m) and was used to build descriptive habitat suitability models for present conditions, allowing us to quantify the importance of each variable to explain the species distribution. The variables included topographical, sedimentological and hydrographical characteristics of the study area. Topographical variables data (depth and slope) were obtained from the high resolution Digital Elevation Model (DEM), derived from data fusion between airborne bathymetric and topographic LiDAR data (Chust et al., 2010a). Slope was derived from depth, using the Spatial Analyst 9.3 extension from Arc-Gis 9.3 software (ESRI®). Maximum current velocity layer was built based on the output obtained from the application of the MOHID water modelling system (explained further in this section) and re-scaled to 1 m resolution under GIS environment using bilinear interpolation method. In order to generate the mean grain size variable, sediment data were obtained from (Valle et al., 2011) (86 samples) and in order to supplement this sediment dataset, 230 surface sediment samples (upper 10 cm) were collected along the intertidal area of the estuary. The grain size distribution of the samples was determined by two techniques according to the fine content of the sediments: samples with <10% of fine sediments were analysed by dry sieving, whereas samples with >10% of fine sediments were analysed using Beckman Coulter LS 13320 laser diffraction particle size analyser (LDPSA). The finest fraction weights obtained by LDPSA were transformed following Rodríguez and Uriarte (2009) to correct underestimation. Mean grain size for all the samples was derived using GRADISTAT software (Blott and Pye, 2001). Mean grain size variable layer was built applying the inverse distance weighted (power 2) interpolation method implemented in the '3D Analyst' extension from ArcGis 9.3.

The second environmental predictor subset was generated with projection purposes, and included variables for present and future conditions (depth, slope and maximum current velocity) modelled using the MOHID water modelling system. This numerical model, designed for coastal and estuarine shallow water applications, is a fully nonlinear, 3D baroclinic finite volume model (available at http://www.mohid.com/). It integrates hydrodynamic and sand transport modules (Malhadas et al., 2009), being able to simulate non-cohesive sediment dynamics in estuaries driven by waves, tide and river flows. MOHID simulates the currents and derived shear stresses at the bottom. Based on the bottom stress, it computes the sediment fluxes allowing the quantification of changes in sediment volume, i.e. changes in bathymetry, which are updated in MOHID at each time step using a mobile bed approach. In this study a 2D configuration of 465 × 1110 grid cells at 10 m resolution and 1 sigma layer for vertical discretization (Arakawa and Suarez, 1983) was defined. The computational domain was configured based on the high resolution DEM (Chust et al., 2010a) as the initial morphological condition of the estuary. On the open ocean

boundary, the tidal forcing was induced considering the tidal components obtained from the Finite Element Solution tide model FES2004 (Lyard et al., 2006). On the landward boundary, the river Oka inflow was imposed assuming a mean annual value of 3.6 m^3 s^{-1} (Uriarte et al., 2004). A period of one month with equinoctial spring tides was chosen to perform the simulations (from 1 to 30 September 2009). The time step was fitted to 2 s and the spin up to 3 days. In order to validate the hydromorphological model, control current measurements were recorded during two tidal cycles at one location of the estuary where *Z. noltii* inhabits, during the spring tides of April 2013. Measurements were acquired with Aquadopp® and RMC 9 self-recording current meters. Location data of the measurements was acquired with the Trimble R6 GNSS system. The bias and the vertical root mean square error (RMSE) (Lazure et al., 2009) computed between the simulated current velocities and field control measurements were 0.8 cm s^{-1} and 5.7 cm s^{-1} respectively, indicating good reliability of simulated values. In order to simulate the SLR effect, three scenarios were established following Valentim et al. (2013): (i) Present, reference scenario without SLR; (ii) scenario with an average SLR of 0.49 m, based upon regional scenarios for the Bay of Biscay (Chust et al., 2010b); and (iii) scenario with an average SLR of 1 m, based upon a global scale scenario (Rahmstorf et al., 2007). The only difference between the three scenarios was the reference sea level used to simulate the tides in the system (i.e. at the sea open boundary, the water elevations over 3 different sea levels that were imposed). Aiming to reduce complexity of the morphodynamic simulations, the variations of seasonal and annual sediment supplies from the rivers and sea were not considered. Therefore, the estuary was assumed to be in a state of dynamic equilibrium (i.e. the long term morphological state of an estuary), where the net sediment deposition is approximately in balance with the net erosion. This assumption implies that the volume of sediments in the estuary is nearly constant.

2.3. Habitat suitability modelling

To assess the future geographical distribution of the climatic niche for *Z. noltii* meadows at its overall biogeographical range level, Generalized Additive Model (GAM) (Hastie and Tibshirani, 1996) and Maximum Entropy model (MaxEnt) (Phillips et al., 2006) habitat suitability modelling methods were selected for comparison purposes. To assess habitat suitability changes derived from the SLR at local scale, the Ecological Niche Factor Analysis (ENFA) (Hirzel et al., 2002) modelling method was also included since it was previously applied to predict *Z. noltii*'s suitable habitat in the same estuary (Valle et al., 2011). The GAM technique (presence/absence method), classified as the semi-parametric extension of Generalized Linear Models (GLMs) (Guisan et al., 2002), allows for nonlinear effects in the predictor variables such as additive functions and smooth components. This technique has been considered for comparison mainly due to availability of realistic absence data, but also because it has been widely used in habitat suitability modelling since it is able to realistically model ecological relationships (Austin, 2002). MaxEnt, a novel machine learning method, based on the maximum entropy principle, is a general purpose method for characterizing probability distributions from incomplete information (Pearson et al., 2007). This method was selected for comparison because it has been found to outperform many different modelling methods (e.g. Elith et al., 2006). ENFA compares, in the multidimensional space of environmental predictors, the distribution of the localities where the target species has been observed to a reference set describing the whole study area (Hirzel et al., 2002).

The GAM models were built using 'mgcv' package (Wood, 2004) implemented in R language, version 2.14.1 (R Development Core Team, 2011), fitting penalised regression splines with a binomial

error distribution. Automated selection of smoothing parameters was fitted up to three degrees of freedom for the models applied at biogeographical range level, and up to five degrees of freedom for the models applied at local scale. The MaxEnt models were developed using the MaxEnt software, version 3.3.3 k. Logistic output format was selected and the number of pseudo-absences was limited to the same number of presence records used in each model. The ENFA habitat suitability models were built using BioMapper software. ENFA was applied selecting the median algorithm, which assumes that the median value for the environmental variable, within the species distribution, is approximately the same as in the study area; it makes no assumptions, based upon the density of the observation/sampling points (Hirzel et al., 2002).

The selection of the variables to be retained on the models applied at the species biogeographical range level was performed under the Akaike's Information Criterion (AIC) allowing the selection of the most parsimonious model. Whereas to build the models at estuary level, firstly all available variables included in the first environmental predictor subset were used in order to assess the contribution of each variable explaining the species distribution for present conditions. Secondly, after selecting the best performing habitat suitability modelling technique, a new model was built including the variables from the second subset, i.e. variables modelled for present and future conditions.

In order to evaluate the models, species distribution data were sorted into three sets, each set containing a random selection of 70% of the observations for model training, and 30% for evaluation. The accuracy of the models was evaluated using Area Under the receiver operating characteristic Curve (AUC) (Fielding and Bell, 1997), and omission and commission errors derived from the confusion matrix (Pearson, 2007). Omission error is defined as exclusion error or underestimation, and commission error as inclusion error or overestimation (Pearson, 2007). Overestimated areas, from which this error is derived, could be interpreted as being potential areas that are not occupied by the species due to, for instance, the dispersal limitation of the species (Guisan and Zimmermann, 2000). Therefore, the relative cost of underestimation was assumed to be higher than that of overestimation (Fielding and Bell, 1997)

2.4. Projection to future conditions

In order to predict *Z. noltii* response to climate change, the selected best models were projected to future conditions, and thresholds were applied to the resulting probability maps. Thresholds were selected by maximizing the agreement between observed and predicted distributions (Pearson et al., 2006). Having defined potential species distribution under present conditions for both analysed levels, and under future conditions, changes on species suitable habitat distribution were assessed by spatial overlap between suitable areas predicted under present and future scenarios. Percentages of gain or loss of suitable space from present to future modelled conditions were calculated assuming unlimited dispersal and no dispersal of the species (e.g. Pearson et al., 2006; Thuiller et al., 2005). In order to quantify the shift of the species when unlimited dispersal was assumed, the geographic centres of gravity of the species' suitable area for present and future scenarios were computed. The centre of gravity was defined as the mean geographic location of a population (Woillez et al., 2009).

3. Results

3.1. Biogeographical range level analysis

3.1.1. Changes in SST under global warming scenario

Differences in average values of mean, maximum, minimum and standard deviation of seawater temperature were shown

between present conditions (2006–2020) and future conditions (2085–2100) (Fig. 2). Northern locations within the area studied were predicted to undergo higher increases in all compared statistics. Whereas along the southern and central locations an average increase of 1 °C was detected.

3.1.2. Habitat suitability model

Mean SST and minimum SST were selected to build the models using GAM and MaxEnt modelling approaches. Both variables significantly explained probability of occurrence ($p < 0.05$) and the AIC values indicated that models including these two variables were the most parsimonious. The GAM model outperformed MaxEnt, with a higher AUC value (0.98 vs. 0.93). Omission errors were very similar for both techniques (0.04 vs. 0.03); whereas the commission error derived from the MaxEnt model was significantly higher (0.05 vs. 0.13). The GAM model was the best model according to the evaluation metrics examined. The model built with both variables explained 80.4% of the species distribution. Comparing single variable models, mean SST explained the greatest deviance in the species occurrence (71.8%), while minimum SST had lower explanatory power (41.7%). *Z. noltii* probability of occurrence decreased with mean temperatures lower than 7 °C and higher than 23 °C, and with minimum temperatures out of the range between 4 °C and 20 °C (Fig. A.1).

3.1.3. Projected future habitat suitability

Under increasing SST scenarios, 81.5% of the species' currently suitable area will remain suitable in 2100 (Fig. 3). Assuming unlimited dispersal capacity of the species, *Z. noltii* could gain 24.3% of its currently suitable area; whereas, if no dispersal is considered, the species would lose 18.5% (Fig. 3). Differences between the centre of gravity of the suitable areas under present and future SST conditions showed that future climate will trigger a poleward shift of 888 km in the suitable habitat of *Z. noltii*; in consequence, currently suitable areas located in the southern limits were projected to be unsuitable for the species by the end of the 21st century.

3.2. Estuary level analysis

3.2.1. Hydromorphological changes under SLR scenarios

Changes in current velocities higher than 10 cm s^{-1}, and even up to 40 cm s^{-1}, were detected in both SLR scenarios (Fig. 4a). These changes were located mainly along the channel in the 0.49 m SLR scenario and throughout the entire estuary in the 1 m SLR scenario. In contrast, changes in erosion and accretion rates were not very important (Fig. 4b): the accretion was found to be lower than 10 cm within the entire estuary. A general erosion trend was detected along the borders of the main channel and
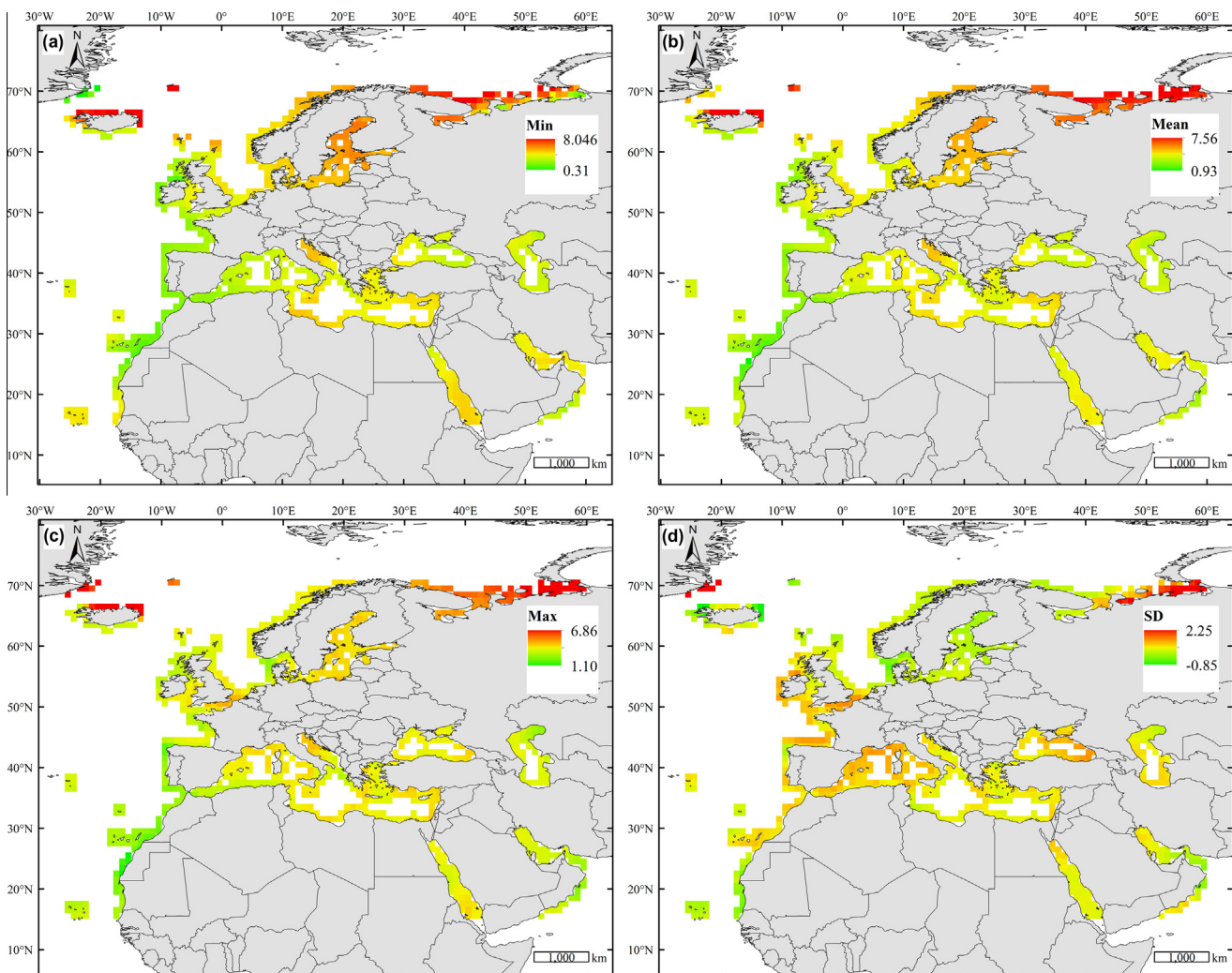

Fig. 2. Range values of changes in seawater temperature from present (2006–2020) to future conditions (2085–2100): (a) Changes in minimum temperature; (b) change in mean temperature; (c) changes in maximum temperature; (d) changes in standard deviation (SD) of mean temperatures.
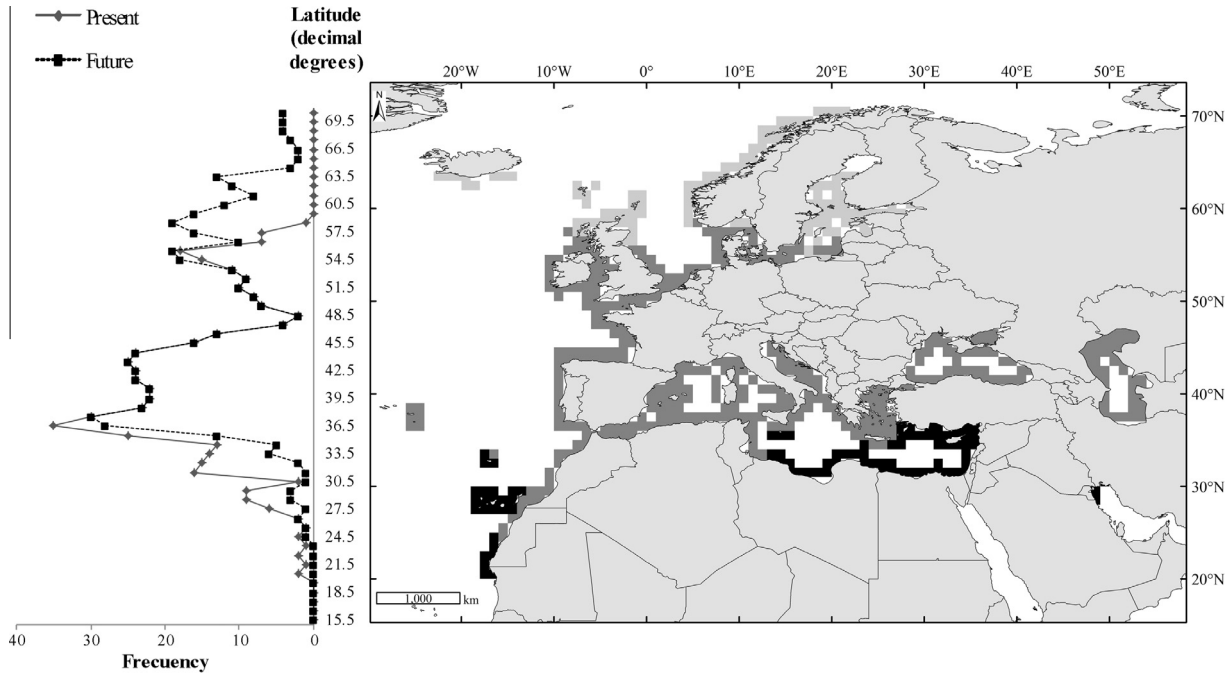
Fig. 3. Estimated changes in the potential species distribution under global warming. In black, currently suitable areas which will disappear in the future scenario (2085–2100); in grey, currently suitable areas which will remain suitable under the future scenario; in light grey, areas currently not suitable which will become suitable in the future. Left plot showing the relative frequency of occurrence in relation to the latitude in the present (grey line) and in the future (black line).
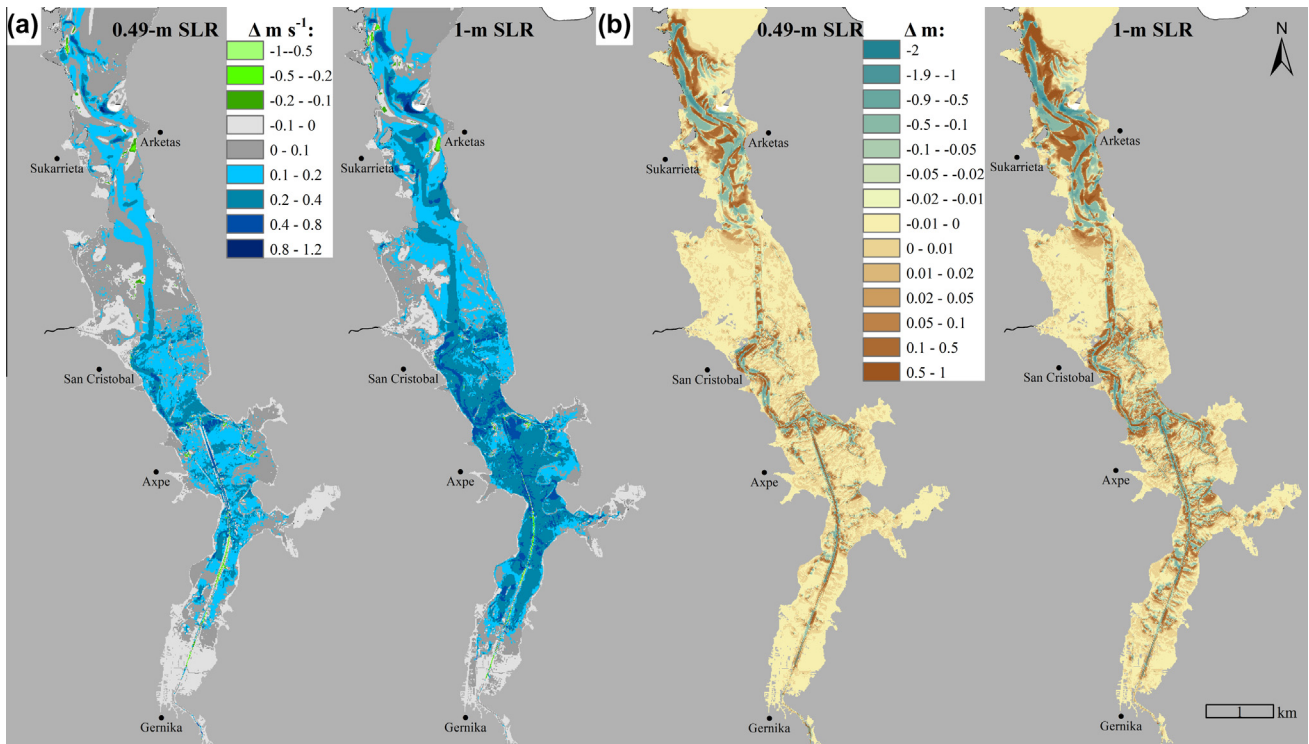

Fig. 4. (a) Changes in maximum current velocity values for 0.49 m sea level rise (SLR) and 1 m SLR scenarios; (b) Changes in erosion and accretion rates for 0.49 m SLR and 1 m SLR scenarios.

accretion in the centre, widening the channel. Derived hydromorphological changes were more evident in the 1 m SLR scenario.

3.2.2. Habitat suitability model

Applied habitat suitability models in the Oka estuary presented a very high accuracy regarding AUC results (average values for each modelling technique were higher than 0.9). The spatial pattern of the predictions was very similar across methods. The GAM model, the one based on presence/absence data, showed the lowest omission error (0.05) followed by MaxEnt model (0.08), whereas ENFA model presented the highest omission (0.15). Commission errors were very low for GAM and MaxEnt

(0.1), being slightly higher for ENFA (0.4). Therefore, the GAM model was selected to define the current species distribution and for projection purposes. The species' presence was limited to narrow ranges of depth (Fig. A.2a); current velocity (Fig. A.2b); and slope (Fig. A.2c), corresponding to intertidal flat areas of the estuary where current velocity is lower than 35 cm s^{-1}. The species, however, occupies a wide range of soft sediments (Fig. A.2d), being mean grain size the less restrictive variable. The full model including all variables explained 96.9% of the species occurrence deviance. Whereas the model built with projection purposes including the variables depth, slope and current velocity explained 92.3% of the species distribution.

3.2.3. Projected future habitat suitability

Under the 0.49 m SLR scenario (Fig. 5a) 76% (110 ha) of the currently suitable area will remain suitable in the future, whilst 24% (35 ha) will become not suitable (Table 1). Assuming unlimited expansion, the species could gain 74 ha (51% of the currently suitable area) (Table 1). These gained areas were detected to be mostly located in the present upper intertidal zone. However, in this estuary there are some areas established within the original upper intertidal and marsh zone which were drained to be used for agricultural purposes traditionally (croplands and pastures) and are protected by walls. These wall-enclosed areas (dashed areas in Fig. 5) will prevent seawater intrusion. Thus, if such barriers are maintained in the future scenario, the gain of suitable areas for the species would be reduced to 55 ha (38% of the currently suitable area) (Table 1). The net gain of the species (calculated by subtraction of the not suitable areas to the gained areas) assuming there were not wall-enclosed areas resulted in 39 ha (27% of the currently suitable area). This net gain might be reduced to 20 ha (14% of the currently suitable area) when considering the presence of the anthropogenic barriers (Table 1).

According to our predictions under the most extreme scenario of 1 m SLR, the currently suitable areas will be reduced by half and meadows located in the outer part of the estuary and near the main channel will be lost (Fig. 5b) (Table 1). As in the previous scenario, some gained areas would be located in the upper intertidal area, although mostly within the above mentioned wall-enclosed areas (dashed areas in Fig. 5). In consequence, if the presence of impervious surfaces is not considered, the species could gain 89 ha (61% of the currently suitable area); but if the wall-enclosed areas are considered, the net gain of the suitable habitats for the species would be drastically reduced to 26 ha (18% of the currently suitable area). Under the 0.49 m SLR scenario, a landward shift of 515 m is expected, and under the most extreme SLR scenario, the shift could reach 1392 m.

4. Discussion

4.1. Projected future distribution under global warming scenario

Temperature has important implications on the geographic patterns of seagrass species abundance and distribution (Walker, 1991), being considered as one of the main variables controlling the seagrasses distribution at global scale (Greve and Binzer, 2004). Waycott et al. (2007) predicted that the greatest impact of climate change on seagrasses will be caused by increases in temperature, particularly in shallower habitats where seagrasses are present. Temperature increase may also alter seagrass abundance through direct effects on flowering and seed germination (Jordà et al., 2012; Massa et al., 2009; Olsen et al., 2012). Since changes in SST would differ geographically the effects would vary between locations and therefore, some meadows could be favoured by the temperature increase; e.g., Hootsmans et al. (1987) found

experimentally that temperatures rising from 10 °C to 30 °C significantly increased *Z. noltii* seed germination. Here, using a highly accurate habitat suitability model based on mean and minimum SST, we projected that the changes in SST derived from global warming would promote an important change in the distribution of the species, triggering a poleward shift of 888 km in the area suitable for the species by the end of the 21st century. This poleward shift was in accordance to our first hypothesis. Although *Z. noltii* can occur in the very shallow subtidal zone, it is typically found in the intertidal region (Green and Short, 2003). Particularly, along the Cantabrian coast, its meadows are confined to estuarine habitats due to the complex and highly variable hydrology of the continental shelf of the Bay of Biscay (Lazure et al., 2009), and the rate of colonizing new estuaries is therefore limited. In this sense it is likely that at higher latitudes, *Z. noltii* populations could not shift their suitable habitat northward at a pace comparable to warming rates, especially in regions where the species is restricted to intertidal estuarine zones. This statement is supported by population genetics studies suggesting a low recolonisation rate from estuary to estuary (Chust et al., 2013; Diekmann et al., 2005), which is related to its main vegetative reproduction strategy (Waycott et al., 2006). Those populations under SST thresholds higher than the temperature ranges required by the species (i.e. southernmost populations) would become extinct by 2100, hence reducing the species climatic niche. The predicted loss of suitable areas at the southern locations is in agreement with Short and Neckles (1999). These authors concluded that, under global climate change, an average annual temperature increase will decrease productivity and distribution of seagrass meadows growing in locations with temperatures above the optimum for growth, or near the upper limit of thermal tolerance. Koch et al. (2013) also stated that many seagrass species living close to their thermal limits will have to up-regulate stress-response systems to tolerate sublethal temperature exposures. Therefore, physiological capacity of adaptation of the species would determine the vulnerability degree of seagrasses to climate change. Although photosynthesis and growth rates of marine macro-autotrophs are likely to increase under elevated CO_2, its effects on thermal acclimation are unknown (Koch et al., 2013). Jordà et al. (2012) reported that it is unlikely that enhanced CO_2 may increase seagrass resistance to disturbances such as warming. Greve and Binzer (2004) considered that the current absence of *Z. noltii* in the northernmost part of Europe might be due to a higher temperature requirement for flowering than *Zostera marina* (a subtidal *Zostera* species). The predicted northward shift of suitable areas for *Z. noltii* could be related to this aspect, since SST warming will allow the species' establishment in that part of Europe. Nevertheless, further research is needed to estimate the dispersal rate of the species in order to confirm the potential habitat reduction and its consequences. Wernberg et al. (2011) found several large and common species retreated south in seaweed communities, which could have substantial negative implications for ecological function and biodiversity. In this sense, the loss of southernmost populations due to climate change may imply future conservation problems. Although southernmost populations could be lost and the colonization of the predicted suitable areas in the northernmost estuaries could be unlikely, a high percentage of currently climatically suitable areas (81.5%) will remain suitable for the species in the future.

4.2. Projected future distribution under SLR scenarios

Elevation relative to mean sea level has been shown to be a critical variable for the establishment and maintenance of biotic coastal communities (Pascual and Rodriguez-Lazaro, 2006). Accounting that the effects of sea level changes are regionally variable (Chust et al., 2010b), we assessed the response of *Z. noltii* to SLR scenarios
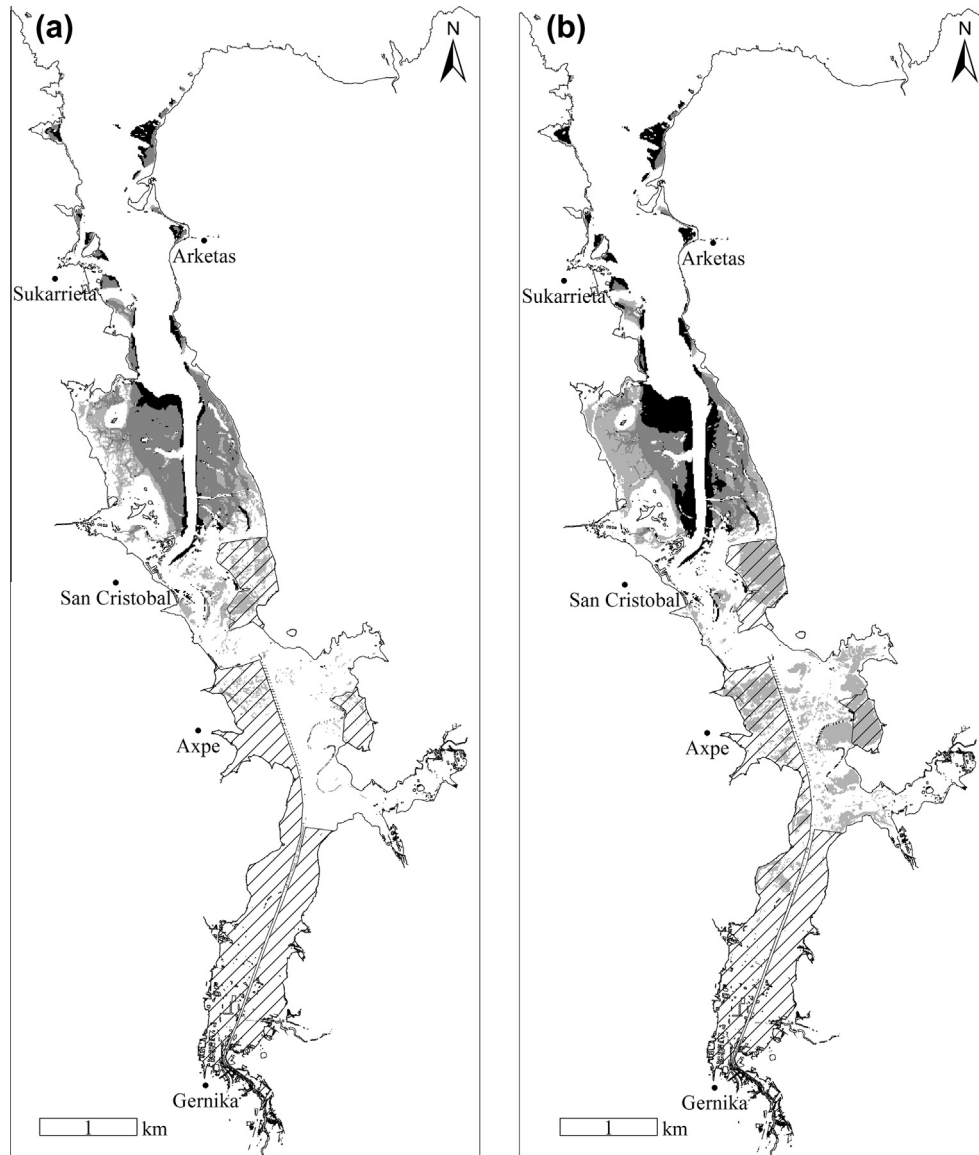
Fig. 5. Estimated changes in the potential species distribution under (a) 0.49 m sea level rise (SLR); (b) 1 m SLR. In black, currently suitable areas which will disappear in the future scenarios; in grey, currently suitable areas which will remain suitable under the future scenarios; in light grey, areas currently not suitable which will become suitable under future conditions. Dashed polygons are wall-enclosed areas.

Table 1
Predicted changes in habitat suitability by 2100 for the 0.49 m sea level rise (SLR) and 1 m SLR scenarios. *Suitable* is the area which will remain suitable in the future. *Not suitable* is the area which will become not suitable in the future. *Gain without walls* is the area which the species could potentially gain assuming there were no wall-enclosed areas. *Net gain without walls* is the net area which the species could gain assuming there were no wall-enclosed areas (*Gain without walls – Not suitable*). *Gain with walls* is the area which the species could potentially gain assuming that the gain area is limited by wall-enclosed areas. *Net gain with walls* is the net area which the species could gain assuming that the gain area is limited by wall-enclosed areas (*Gain with walls – Not suitable*). Values in ha and in relative% of the currently suitable area (145 ha).

	0.49 m SLR		1 m SLR	
Suitable	110 ha	76%	70 ha	48%
Not suitable	35 ha	24%	75 ha	52%
Gain without walls	74 ha	51%	164 ha	113%
Net gain without walls	39 ha	27%	89 ha	61%
Gain with walls	55 ha	38%	101 ha	70%
Net gain with walls	20 ha	14%	26 ha	18%

at estuary level. Only one estuary was studied due to the need of high resolution data and the computational requirements for modelling hydromorphological changes. We showed that *Z. noltii* will gain suitable habitat within the Oka estuary due to SLR. The local geomorphology of this estuary favoured an expansion of intertidal areas, triggering an increase in the suitable habitat for the species. Therefore, as expected by our second hypothesis, SLR and derived changes in current velocities will redistribute suitable habitat of the species, inducing the landward migration of the species. Suitable intertidal areas will increase by 27% (0.49 m SLR) and by 61% (1 m SLR) (Table 1). Although, as expected by Short and Neckles (1999), shifting of seagrass beds landward will be impeded by anthropogenic constructions. This has been also found for the Oka estuary, where, if no actions are undertaken, anthropogenic barriers would reduce the increase in suitable habitat from 27% to 14% (0.49 m SLR) and from 61% ha to 18% (1 m SLR) (Table 1). Shaughnessy et al. (2012) found that the strength of the extinction effect depends on how much of the intertidal and upland areas can

accommodate a landward shift in seagrass distribution. In the case of the Oka estuary, there is a large upper intertidal area available which will allow the species' landward shift. Nevertheless, impervious surfaces built within the estuary (dashed areas in Fig. 5) would drastically reduce the future suitable area. Saunders et al. (2013) concluded that managed retreat of the shoreline, such as removal of impervious surfaces, could potentially reduce the overall decline of seagrass in Moreton Bay (Queensland, Australia). Considering the differences in the future suitable area in the Oka estuary with and without wall-enclosed areas, we can conclude that in addition to restoration tasks in other estuaries, environmental management measures, such as removing anthropogenic barriers, could be taken in order to assist the landward migration of this endangered species in the future.

Our results differed somewhat from those found by Chust et al. (2011) in the same estuary. Chust et al. (2011) projected a reduction in suitable habitat of 40% by the end of the 21st century. This is explained by differences in the extent of the study area considered, which was limited in the previous study. Also, our new results benefited from improvements in: (i) selection of the most accurate habitat suitability model; (ii) simulations of the hydromorphological changes of the estuary; and (iii) coupling of hydromorphological model derived simulations with the selected habitat suitability model. Some of these improvements were already suggested in Chust et al. (2011) and they all have led to more accurate and reliable results. Under the present research, 24% of the currently suitable habitat will become unsuitable for the species (Table 1), mainly due to the simulated increase in maximum current velocities along the areas located close to the main channel of the estuary. This is consistent with the well documented influence of the water dynamics on seagrass distribution (e.g. Fonseca and Bell, 1998). Encouraging results regarding the potential of *Z. noltii* to recover have been reported by Barillé et al. (2010) and Dolch et al. (2013). The former found a steady and linear increase in *Z. noltii* meadow areas within Bourgneuf Bay (France), being tidal flat accretion one of the most significant variables explaining the observed expansion downwards. The latter found a recovery of mixed intertidal beds of *Z. marina* and *Z. noltii* in the North Frisian Wadden Sea (Germany), likely driven by the decline of nutrient loads over the last 20 years. Marques et al. (2003) also concluded that seagrass beds of *Z. noltii* can recover from the stress of eutrophication when measures are put in place to manage the system. Thus, considering that the water quality in the Basque estuaries has been improving in recent years (Tueros et al., 2009), and that full recovery of many coastal marine and estuarine ecosystems can take a minimum of 15–25 years after over a century of degradation (Borja et al., 2010), results from these authors strengthen the confidence in the possible colonisation of the projected future suitable habitat. However, apart from water quality improvement, management measures to reduce the threat by anthropogenic impact (Chust et al., 2009) also must be taken.

4.3. Model performance

Habitat suitability models performed well and accurately described species distribution at both levels (biogeographical range and estuary level). Based upon the AUC evaluation method, a consistently high predictive accuracy was found for all the applied habitat suitability models, the GAM technique (based on presence/absence data) being the best performing technique. To date, many authors have performed comparisons between multiple modelling techniques (Brotons et al., 2004; Elith and Graham, 2009; Guisan et al., 2002; Hirzel et al., 2001; Oppel et al., 2012) and presence/absence methods generally outperformed presence-only methods. In this sense, we found poorer accuracy in the ENFA method, which could be explained by the fact that it

is a strict presence-only method and does not take into account the areas from which the species might be absent, being less conservative in estimating the species' realised niche (Brotons et al., 2004). This has been evidenced in our study by the higher commission error detected for the ENFA technique. Although MaxEnt and GAM modelling techniques presented very similar AUC values, the GAM technique showed a higher discrimination power judged by the omission and commission errors. Downie et al. (2013) and Powell et al. (2010) also found the GAM model to outperform the MaxEnt technique. Therefore, based on our results, if good quality presence/absence data is available, presence/absence methods are thoroughly recommended since they are able to generate statistical functions or discriminative rules that allow habitat suitability to be ranked according to distributions of presence and absence of species (Brotons et al., 2004; Guisan and Zimmermann, 2000).

4.4. Assumptions, limitations and uncertainty

Forecasts of species distributions under future climates are inherently uncertain (Wenger et al., 2013). Here we combined several models: (i) a general climate model, applied to predict the changes in SST; (ii) a hydromorphological model, applied to predict the changes derived from the SLR; and (iii) habitat suitability models applied to project future species distribution. Although climate model simulations were compared within the defined reference period and hydromorphological simulations were confirmed to be reliable based on field validation, uncertainties could arise regarding future simulations due to model assumptions. For instance, to perform the hydromorphological modelling, as in other previous studies (e.g. Lopes et al., 2011; Valentim et al., 2013), dynamic equilibrium of the estuary was assumed and this could have led to an underestimation of sediment accretion in the intertidal flat. In this sense, complex aspects of sedimentation transport are not yet fully understood and formulas are therefore approximations from where errors in sediments flux estimations are usually derived (Lopes et al., 2011). Habitat suitability modelling also requires assumptions to be made (Elith and Leathwick, 2009). In this context, extensive literature covers the uncertainties arising when the models are applied with forecasting purposes (e.g. Heikkinen et al., 2006; Sinclair et al., 2010). Although model ensembles for forecasting are recommended by some authors to reduce uncertainty derived from variability across modelling techniques (e.g. Thuiller et al., 2009), our approach based on the selection of the best performing model, together with its high accuracy, supports the reliability of the results obtained. As pointed by Whittaker et al. (2005), limitations of the models must be understood for a proper interpretation of the results. Lastly, besides climate, there are different types of non-climate driving forces influencing the changes exhibited by species (Rosenzweig et al., 2007). Nevertheless, accounting for the inherent caveats, our results could be considered as a first approximation to how changes in seawater temperature and in sea level could affect *Z. noltii* meadows distribution. In addition, the information generated might support ecosystem management decisions to be undertaken at local scale, such as conservation actions towards the sites where the habitat would remain suitable for the species under climate change.

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Appendix A

See Figs. A.1 and A.2.

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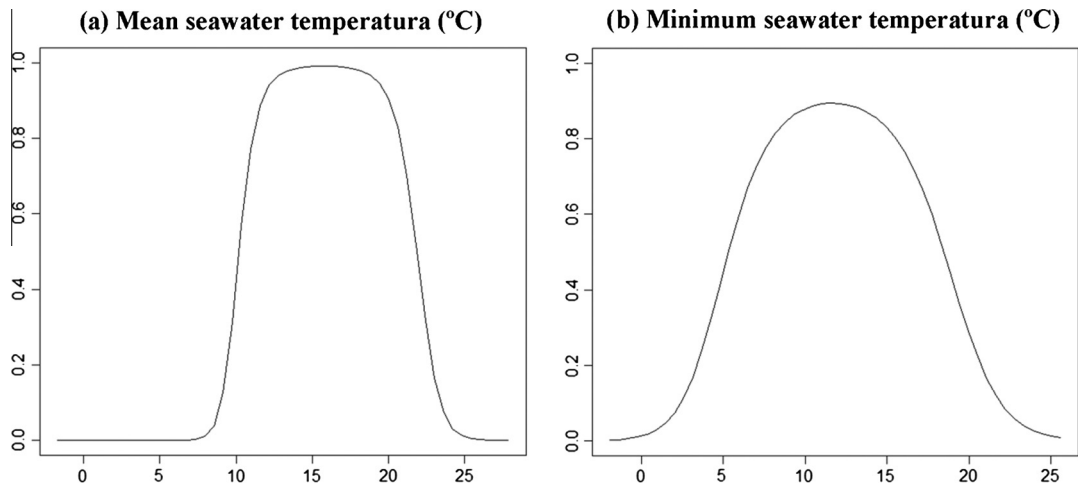

Fig. A.1. *Zostera noltii*'s response curves derived from the habitat suitability model applied at biogeographical range level of the species.
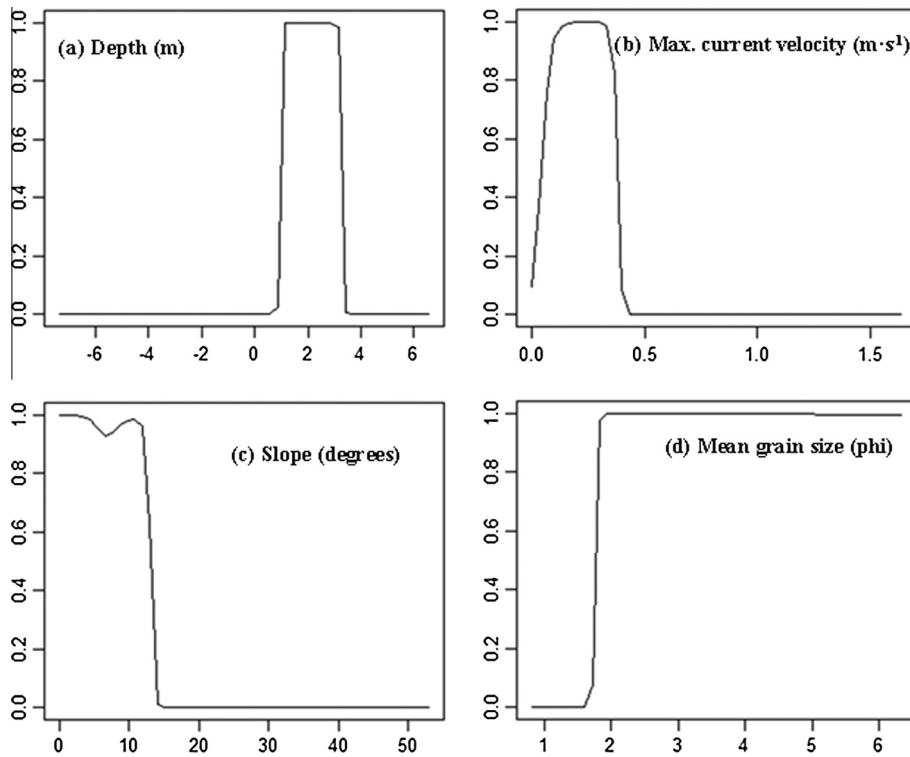

Fig. A.2. *Zostera noltii*'s response curves derived from the habitat suitability model applied in the Oka estuary.

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