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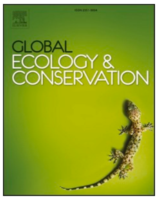

Short communication

Predicted regime shift in the seagrass ecosystem of the Gulf of Arguin driven by climate change

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ABSTRACT

The Banc d′Arguin is a marine ecosystem of global conservation significance, the largest bird sanctuary of western Africa, supported by one of the most extensive seagrass beds in the world composed by three seagrass species, two temperate near their southern limit (*Zostera noltei* and *Cymodocea nodosa*) and one tropical at its northern limit *(Halodule wrightii)*. Here we predict the fate of this seagrass ecosystem under climate change scenarios during the 21st century, using species distribution models and sea level rise estimates. We forecast a probable decline in total seagrass area of 3340 Km^2 (78%) by 2100, involving the loss of both temperate seagrasses (*Z. noltei, C. nodosa*), the foundational ecosystem components. By 2050, only the tropical species *(H. wrightii)* would remain, which forms thin and sparse shallow stands functionally distinct from the previous tall dense meadows that span wider vertical ranges. Intertidal flats, the essential bird foraging habitats, would become unvegetated and also suffer a major reduction in area (114 km^2 by 2050, 587 km^2 by 2100). The large projected loss of foundational seagrass species portends a collapse of major ecosystem functions with profound impacts on biodiversity, fishery resources and ecosystem services.

1. Introduction

The Gulf of Arguin on the western coast of Africa (Mauritania), facing one of the richest upwelling fishing regions, contains one of the most extensive pristine seagrass habitats on Earth (Trégarot et al., 2021). These provide major feeding and/or breeding sites for a wide range of marine species, including seabirds, turtles, endangered elasmobranchs and species of commercial interest (Araujo and Campredon, 2016). The Parc National du Banc d′Arguin (PNBA, comprising 12,000 km^2 of which half are marine) is arguably the most

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important coastal wetland in Western Africa, recognized for its unique universal value by the UNESCO's Marine World Heritage Programme. Moreover, it is a globally significant hotspot for blue carbon, as it ranks as the third largest area of seagrass and the third largest carbon stock, as well as the fifth most extensive tidal marshes and carbon stocks among these UNESCO sites (Duarte et al., 2021). PNBA, also a Ramsar Wetland of international importance and a WWF "Gift to the Earth", offers protection to the seagrass banks and the associated fauna (including threatened birds, fish and marine mammals). For example, the PNBA is recognized as the most important habitat of the Western Atlantic for nesting birds and Palaearctic migratory waders (https://whc.unesco.org/en/list/506/).

Despite their extreme ecological and socio-economic value (Trégarot et al., 2021), the vast seagrass ecosystem of the Gulf of Arguin occurs in marginal conditions, since two (*Zostera noltei* and *Cymodocea nodosa*) of the three seagrass species are temperate taxa at their trailing (southern) edges and vertically constrained by light availability and a low elevation tidal flat. These constrains render this seagrass ecosystem particularly vulnerable to both increasing sea surface temperatures (SST) and sea level rise (SLR) with climate change. Here, we forecast the climate-driven changes in seagrass habitat using species distribution models (SDMs) for future climate and SLR regimes. We develop predictions for two scenarios used by IPCC as trajectories of concentrations of greenhouse gases (named RCPs: Representative Concentration Pathways) by 2050 and 2100 (https://www.ipcc-data.org). We select two contrasting cases of the IPCC, the RCP2.6 (where radiative forcing, a measure of the Earth's net gain in sunlight energy causing warming, peaks lower, at 2.6 Wm^{-2}), and RCP8.5 (radiative forcing reaches >8.5 Wm^{-2}), by 2100. This way we examine the effect of ocean warming and sea level rise on the distribution of seagrasses according to two contrasting future possible scenarios caused by lower (RCP2.6) and higher (RCP8.5) greenhouse gas emissions, and at two moments of the time series (2050, 2100).

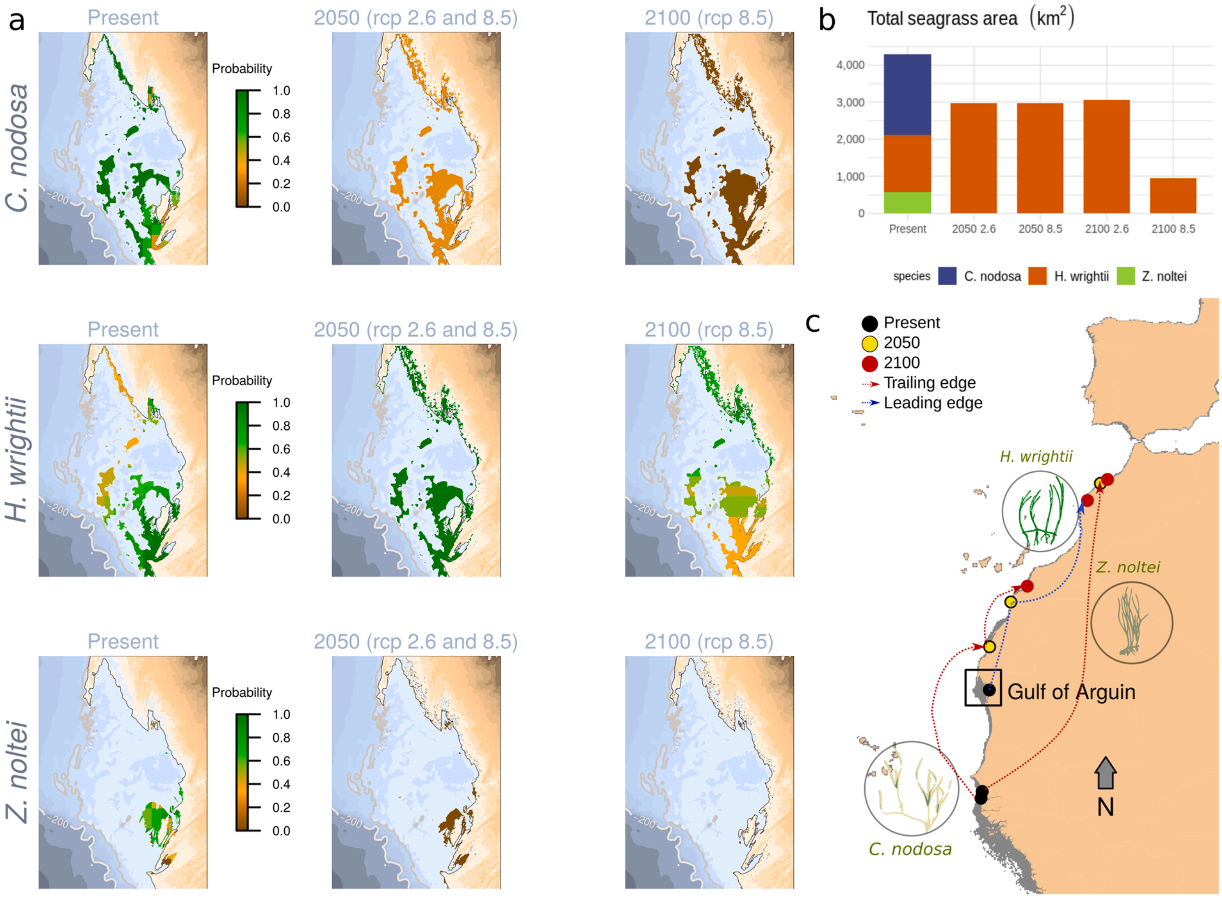

Fig. 1. Seagrass species redistribution considering future climate change and sea level rise (SLR) in the Gulf of Arguin. a) Probability of occurrence predicted by the ensembles of species distribution models (SDMs) was low for *Cymodocea nodosa* and *Zostera noltei* and higher for *Halodule wrightii*. In addition, SLR is predicted to increase subtidal habitat for *C. nodosa* and *H. wrightii* and reduce intertidal habitat for *Z. noltei*. b) Stacked bar chart shows the overall change in seagrass extension considering both SLR and future conditions after transforming the predicted probabilities of occurrence into binary maps. c) Predicted species' range shift: "Present" dots represent the southernmost known locations for *C. nodosa* and *Z. noltei*, and the northernmost for *H. wrightii* in the North West African coast. Arrows show the maximum latitudinal shift of the trailing (southern, red arrows) edge for *C. nodosa* and *Z. noltei*, as well as the leading (northern, blue arrows) edge for *H. wrightii* by 2050 and 2100. Coastal waters within the depth limits of the species and analysed in the species distribution models are shown in grey.
Cartoons of the species were modified from http://texasseagrass.org and https://ian.umces.edu/.

2. Material and methods

2.1. Biological data of seagrass species

To produce the SDMs we used occurrence data for the entire range per species, obtained from literature, from our field surveys along the Banc d′Arguin, and online databases such as the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), the European Marine Observation and Data Network (EMODnet; http://www.emodnet.eu/), and the Ocean Biogeographic Information System (OBIS; www.iobis.org). Records were checked to remove dubious locations, aquarium specimens and misidentifications. Species occurrences are presented in Appendix A. From all the records compiled, only one observation per 5′ pixel (~9.2 km at the equator) was considered in the modeling process to reduce the effect of sampling bias: 415 for *Z. noltei*, 71 for *H. wrightii*, and 211 cells for *C. nodosa*. The coastal cells for the global SDMs were delimited using a 40 m depth threshold from the 30 arc-seconds resolution GEBCO's gridded bathymetric data set (https://www.gebco.net/). These SDMs were applied here to forecasts in Gulf of Arguin (20.6ºN, 16.49ºW; Fig. 1).

In the PNBA field surveys, we searched by snorkelling or dredging for the lower depth limit of seagrasses at the south border near El Mamghar, the north border near Cap Sainte-Anne, and at the islands Arguin, Tidra, Zira, Kiji, Kiaone, Niroumi, Nair, and Arel. Due to lack of another reference system, depths were approximately estimated relative to the transition between *Z. noltei* (intertidal) and *C. nodosa* (subtidal) as zero level. At each site, we determined the maximum leaf length and shoot density within 3–5 cores (12 cm diameter) for each species.

2.2. Environmental data

After checking Pearson correlation ($r \leq |0.8|$) of marine variables available for future climate scenarios: monthly average of sea surface temperature (SST maximum, minimum, mean and range) and salinity, we selected minimum and maximum SST and salinity, previously validated predictors for several seagrass and seaweeds (Chefaoui et al., 2018, 2019). Present values were obtained from Bio-ORACLE v2.0 (Tyberghein et al., 2012; Assis et al., 2018), future values were ensembled from five Ocean General Circulation Models (see Chefaoui et al., 2018 for details).

2.3. Species distribution models (SDMs)

We predicted current and future distributions for the three seagrass species by performing ensemble modelling of six algorithms with the "biomod2″ package (Thuiller et al., 2019) for R (R Core Team, 2020). For the ensembles, six presence–absence algorithms were computed: generalized linear model (GLM), generalized additive model (GAM), flexible discriminant analysis (FDA), generalized boosting model (GBM), randomForest (RF), and multiple adaptive regression splines (MARS). We extracted at random twice the number of pseudoabsences as presence cells for each species, and two sets of pseudoabsences were created to increase randomness. A total of 60 models were computed for each species (6 modelling techniques x 5 iterations x 2 pseudoabsence sets). We split data into a calibration (70%) and a validation set (30%) in each of the 5 iterations performed for each set of pseudoabsences. To evaluate the relative importance of the variables, we used three iterations and obtained an importance value from 0 to 1 (highest importance). Model performance was evaluated using true skill statistic (TSS) (Allouche et al., 2006), area under the receiver operating characteristic (ROC) curve (AUC), and their derived sensitivity (presences correctly predicted) and specificity (absences correctly predicted) measures (Fielding and Bell, 1997). Ensemble for the present was computed using an average of binary predictions ("committee averaging") of the models achieving TSS $\geq$ 0.65. The ensembles were projected to four future scenarios: RCP 2.6 and RCP 8.5 by 2050 and 2100. Clamping masks were used to assess the uncertainty involved in the extrapolation of models to future conditions, determined as the difference in the values of the variables between the novel scenarios and the training range (Fig. B.1., Appendix B). Variable importance in the ensembles was calculated by the correlation between a model without each variable and the full model (Liaw and Wiener, 2002; Thuiller et al., 2019). Predicted occurrence probabilities were transformed into binary maps (presence–absence) at thresholds that optimized ROC and TSS (Thuiller et al., 2019). The lost, gained and stable predicted habitats between the present and each future scenario were estimated by comparing binary predictions, and the change in occurrence probability.

2.4. Digital elevation model (DEM), sea level rise analysis and seagrass meadow extension

To estimate the current and predicted extension of seagrass habitat in the Gulf of Arguin, we delimited the obtained SDMs with the sea level rise (SLR) estimated from regional projections under the RCP2.6 and RCP8.5 scenarios by 2015 and 2100, together with depth ranges observed at the Banc d′Arguin for each species.

First, to delineate the vertical niche for each species conditioned by future SLR in the Gulf of Arguin, we produced a fine scale DEM by coupling bathymetric and elevation data from different sources. For coastline and bathymetric data, we used the map at 0.0005 degrees resolution of the Gulf of Arguin provided by Alemán et al. (2014). Since no bathymetric or land data for intertidal habitat were available, we digitized intertidal habitat under present conditions combining Google Earth Pro Satellite imagery and the information provided by the Map of Banc d′Arguin (http://www.effectivempa.noaa.gov/sites/bancdarguin.html). The distance to the coast calculated with the "distance" function from the "raster" package (Hijmans, 2020) for R was used to produce a gradual DEM for the intertidal ranging from half the mean tidal range (−0.5 m) reported for the Gulf of Arguin in Bird (2003) to 0 m. To produce a fine resolution coastal DEM, we extracted elevation data from 32,371 points on land using Google Earth Pro. Elevation was corrected using the free software GPS visualizer (https://www.gpsvisualizer.com/) which uses the best available DEM data from NASA sources. Then, elevation data was interpolated using the Natural Neighbour method to a fine scale grid (0.0005 degrees) using the open software SAGA v 7.3.10 (http://www.saga-gis.org).

Second, future sea levels (SLR) together with species depth ranges were applied to our DEM to constrain the SDMs and estimate the change in seagrass habitat across time. Mean regional variations in SLR for each RCP scenario (Oppenheimer et al., 2019) for the Gulf of Arguin were: 0.3 m (RCP2.6, 2050), 0.4 m (RCP8.5, 2050), 0.7 m (RCP8.5 2100). Species depth ranges were estimated through our PNBA field surveys, which found *Z. noltei* only in the intertidal, and a depth range for *C. nodosa* and *H. wrightii* generally shallower than 4 m throughout the Gulf of Arguin. This is a conservative depth aimed to provide the maximum possible estimate of seagrass area, which was often about 2 m for *C. nodosa* and < 1 m for *H. wrightii* (both at low tide), in the very turbid seawater of the Gulf of Arguin. Because the small *H. wrightii* presently occurs subtidally in mixed beds with the much larger seagrass *C. nodosa*, likely constrained in depth by canopy competition, we considered the same potential depth limit of 4 m for both subtidal seagrass species for estimates of potential future cover area, as *H. wrightii* might hypothetically extend deeper in the absence of *C. nodosa*. The seagrass extension across time considering climate change and SLR was calculated from the binary predictions as the number of suitable cells and transformed into square kilometres. All spatial analyses were performed in R using the "raster" package (Hijmans, 2020).

3. Results

Our results predict for the Gulf of Arguin a contraction of the ranges of temperate *C. nodosa* and *Z. noltei* (Fig. 1 and Figs. B.2–B.4. Appendix B) at their trailing (southern) edges, whereas the tropical *H. wrightii* would experience a northward expansion beyond its current northern edge at the Gulf of Arguin. Therefore, only *H. wrightii* would remain under future scenarios, with its probability of occurrence increasing by 2050 and under RCP 2.6 by 2100 (Fig. 1). The performance of the models was strongly validated (test AUC above 0.9, TSS above 0.7 for all species; Table B.1., Appendix B), with low uncertainty detected by the clamping masks, which did not affect the study area (Fig. B.1., Appendix B). Minimum SST was the most relevant variable for *H. wrightii*, maximum SST for *C. nodosa,* and salinity for *Z. noltei*, but similar to the contributions of both minimum and maximum SST in the ensembles (Table B.1., Appendix B). In the Gulf of Arguin the mean value of maximum SST is projected to increase from 25.06 °C in the present to 29.80 °C under RCP 8.5 by 2100; while the mean minimum SST would increase from 18.26 °C to 23.14 °C. Salinity would experience a lesser increase, from a mean value of 35.9–36.6 (Table 1). SLR also played an important role in constraining the available habitat. Subtidal habitat ranging from the intertidal to -4 m, currently extending over 2477 Km^2, would increase 22% by 2050 and from 24% to 35% by 2100. Intertidal habitat comprising 811 Km^2 at present, however, is expected to suffer a reduction in extension by 14% by 2050–29% and 72% by 2100, despite flooding of new areas. The net result is a projected decline in total seagrass area from the present 4295 km^2 to 2977 km^2 by 2050, and further down to 9,55 km^2 by 2100 under RCP 8.5 (Fig. 1).

The three seagrass species build canopies with distinct characteristics in the Banc d'Arguin (Figs. 2 and 3). Leaves of *C. nodosa* are much wider than those of *Z. noltei* and the even thinner *H. wrightii*. Across all sites, despite variability between locations, *C. nodosa* is always longer (maximal leaf length 38.4 ± 7.9 cm), compared with *Z. noltei* (19.6 ± 2.5 cm) and the shorter *H. wrightii* (14.7 ± 1.8 cm). The intertidal, *Z. noltei* forms meadows with very high density (1286.6 ± 273 shoots per m^2) in comparison with the subtidal species *H. wrightii* (376.8 ± 25.8) and *C. nodosa* (335 ± 58.3). Thus, the temperate *C. nodosa* grows longer and wider leaves than all, *Z. noltei* forms larger shoot densities than all, whereas the tropical *H. wrightii* constructs a smaller habitat structure with short thin leaves and low shoot densities (Figs. 2 and 3).

4. Discussion

A regime shift in the seagrass ecosystem of the Gulf of Arguin is expected considering the effects of climate change and sea level rise (SLR). Our projections foretell a major loss of ecosystem structuring vegetation, so that the previous tall and broad-leaved *C. nodosa* canopies in the subtidal zone will retain only the shorter and thin tropical *H. wrightii.* The future predicted expansion of *H. wrightii* (around 95% to occupy up to 3069 km^2 in the Gulf of Arguin; Fig. 2) is in turn conditional on the species being able to expand down into the same depths as *C. nodosa* once light competition by this larger species is removed. The massive intertidal seagrass meadows of *Z. noltei* will become unvegetated tidal flats, and the odds of this habitat loss derived from climatic unsuitability are reinforced by the

Table 1

Range values (min.-max.) in the Gulf of Arguin for the predictors used in the species distribution models of *Cymodocea nodosa, Zostera noltei* and *Halodule wrightii*. Global species ranges are the thresholds found for the predictors under present conditions in the cells with occurrence records in their entire range of distribution. All metrics of environmental variables were derived from the time series of monthly climatologies described in Methods. SST: sea surface temperature.

	Ranges of variables in Gulf of Arguin					Global species ranges		
	Present	2050 (RCP 2.6)	2050 (RCP 8.5)	2100 (RCP 2.6)	2100 (RCP 8.5)	*C. nodosa*	*Z. noltei*	*H. wrightii*
Maximum SST (°C)	21.68–29.29	27.47–28.18	27.80–28.60	27.34–28.12	29.36–30.20	20.73–31.0	14.22–29.62	25.83–32.26
Minimum SST (°C)	17.11–19.60	20.64–21.70	20.80–21.87	20.82–21.87	22.58–23.69	6.55–22.51	-1.66–21.66	13.37–27.57
Salinity (unitless)	35.73–36.13	36.38–36.51	36.28–36.41	36.44–36.55	36.57–36.65	17.50–39.33	6.01 – 39.38	30.16–37.13

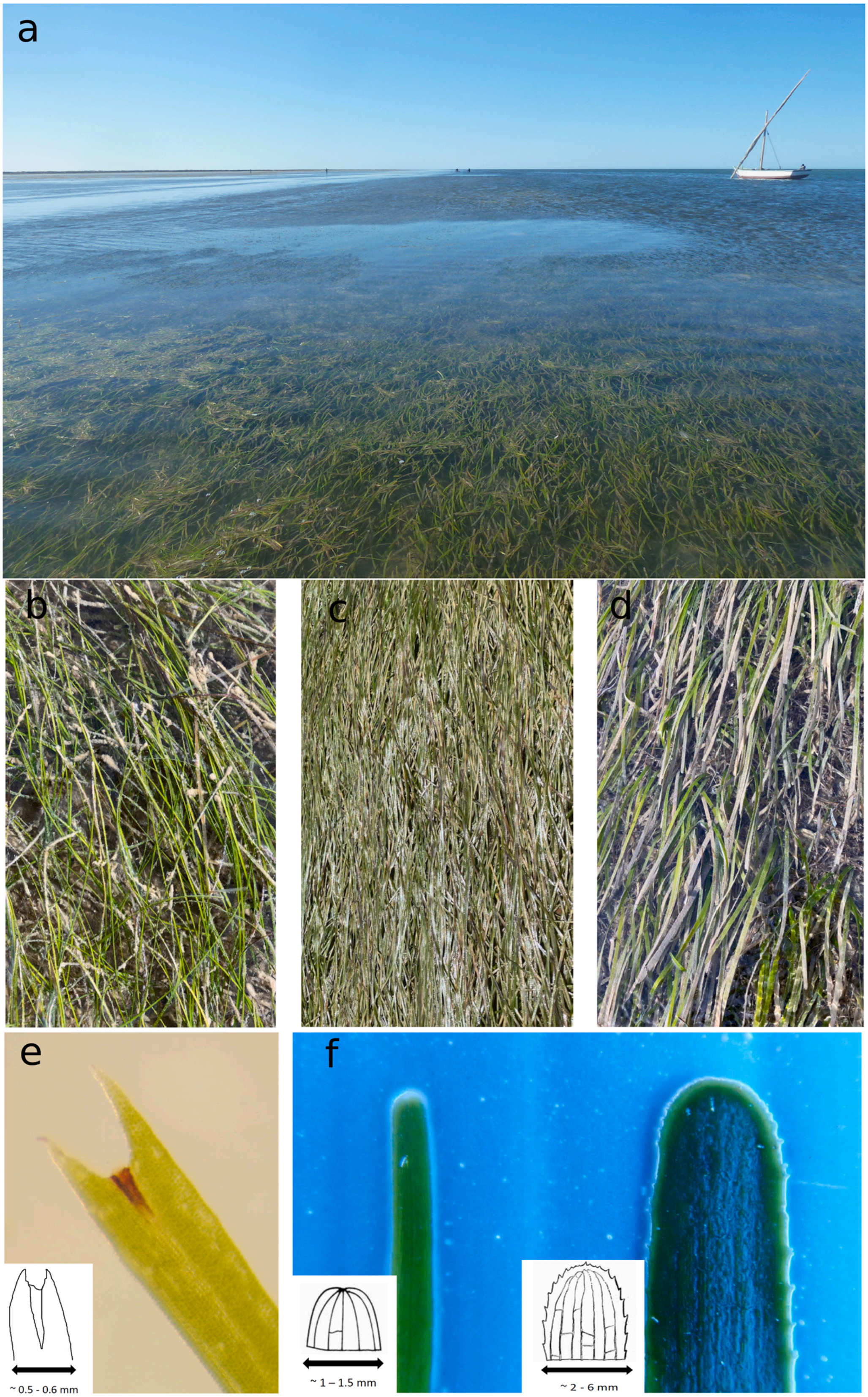

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Fig. 2. Leaf and canopy structure of the three seagrass species of Banc d′Arguin. *Cymodocea nodosa* meadow at its upper depth limit (a). Seagrass canopy density and leaf tip of *Halodule wrightii* (b, e), *Zostera noltei* (c, f (left)), and *Cymodocea nodosa* (d ,f (right)). Photo credits: (a-e) authors, (f) Aschwin Engelen.
Drawings of seagrasses tips were modified from Creed et al. (2016) and http://www.floraiberica.es/.

huge reduction of the extensive intertidal flats caused by SLR, predicting a future reversal of a recently reported increasing trend (El-Hacen et al., 2020). Although uncertainties in the extension of future intertidal habitat exist due to the lack of accurate bathymetric data for the intertidal bottom, we found that SLR would increase the extension of subtidal habitat by one third, since coastal and current intertidal regions might be flooded. Our digital elevation model identified the habitat most affected by SLR to be “sabkha”, halophyte communities growing in seasonal flooding areas separated from the sea by a dune ridge (Gourmelon et al., 2006) and the extensive intertidal flats around Tidra Island (Fig. 2).

Assessing the impact of climate change on marine biodiversity is particularly urgent in developing countries of tropical regions, in which trailing edges of species are shifting northwards (Worm and Lotze, 2021). If a very shallow elevation profile is also present in the coastal trailing edge of several species, as is the case of Banc d′Arguin, then the cumulative effects should be assessed for the planning of adaptation strategies. This is to our knowledge the first study identifying the vulnerability of the biogeographical trailing edges to the combined effect of climate change and SLR using model estimates.

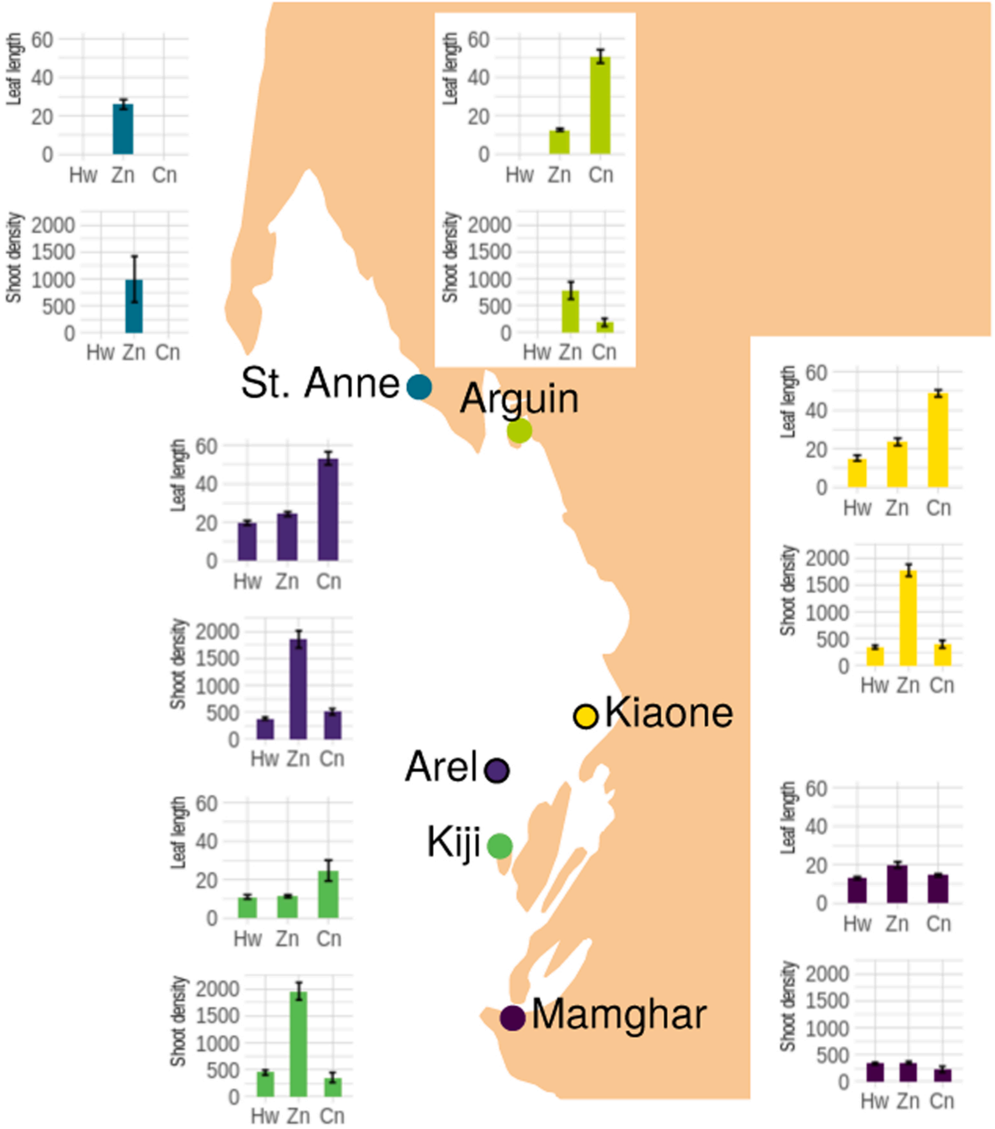

Fig. 3. Maximum leaf length (cm) and shoot density (shoots·m^{-2}) of the three seagrass species of Banc d′Arguin, at the surveyed sites where seagrass was found. Cn: *Cymodocea nodosa*; Hw: *Halodule wrightii*; Zn: *Zostera noltei*.

The nearly complete loss of two canopy-forming seagrass species (*Z. noltei* and *C. nodosa*), partially replaced by *H. wrightii*, a small, patchy seagrass species, erodes the Gulf of Arguin's capacity to continue supporting species of conservation interest. The disappearance of seagrass meadows will threat resident and nesting grounds for migratory birds within the East Atlantic Flyway. Intertidal seagrass habitats of the Banc d′Arguin offer a varied range of feeding sources for wintering shorebirds, including bivalves, crustaceans, insects, gastropods, polychaetes, and even *Zostera* spp. rhizomes (Lourenço et al., 2016). Despite seagrasses *per se* not being the main food for shorebirds, a significant portion of the zoobenthos uses seagrass as food source (Honkoop et al., 2008). Molluscan species richness and total biomass are higher in seagrass than in bare habitats in the Banc d′Arguin (Honkoop et al., 2008). Thus, the loss of seagrasses could decrease the benthic populations of prey species dependent on seagrasses that are consumed by wintering shorebirds, as is the case of the bivalve *Dosinia* sp. preferred by the Red Knot at Banc d′Arguin (Honkoop et al., 2008; Onrust et al., 2013; El-Hacen et al., 2020). Besides, these shifts could trigger the invasion of other species. In addition, subtidal marine fauna would likely be affected, as these are major feeding grounds for large populations of the herbivorous endangered green turtles (*Chelonia mydas*), and are nursery grounds for many fish species, including dozens of elasmobranch species with IUCN status of vulnerable, endangered or critically endangered.

The loss of these vast seagrass meadows would be especially tragic for local communities, preventing their nursery services for productive artisanal fishery upon which local households depend for subsistence in this extremely arid country. Moreover, the dramatic reduction in seagrass area with climate change in the Banc d́Arguin represents the loss of a globally-relevant carbon sink and brings about risks of emissions of their vast carbon stocks presently stocked, once the seagrass cover is lost (Pendleton et al., 2012). Climate change may, thus, lead to the functional loss of one of the most important marine ecosystems along the Western African coast and a site of global conservation significance. Since additional local stressors could aggravate the effect of ocean warming and SLR, regular frequent monitoring of the vulnerable seagrasses by local agencies is increasingly important.

With the loss of the major foundation species of the Banc d'Arguin, Mauritania will suffer a great loss caused by climate change despite having contributed little to global greenhouse gas emissions. Preventive or adaptive measures are limited at the local scale of the Banc d′Arguin. The best and possibly unique solution for this ecosystem is mitigating climate change along the most ambitious goals of the Paris Agreement (to limit global warming to 1.5ºC, compared to pre-industrial levels). This is an imperative measure, the only that could still help the most climate-vulnerable countries like Mauritania, that provide major marine ecosystem services to the global world.

CrediT authorship contribution statement

RMC, CMD and EAS conceived the study, interpreted the results, and revised the text. RMC analysed the sea level rise and species distribution models and made the figures. RMC and EAS wrote the manuscript. RMC, EAS, AIT, DGF contributed to the acquisition of the seagrass occurrence data and EAS, MASC, MAB, conducted the work in the Banc d′Arguin.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01890.

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