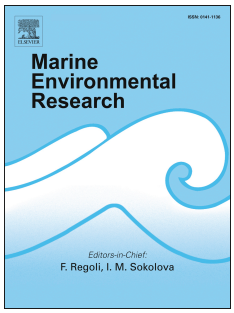

The impact of climate change on the geographical distribution of habitat-forming macroalgae in the Rías Baixas

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MD, BM, MdC, RMV and MGG conceived and designed the study. MD, MdC and MGG conducted the numerical simulations. BM and RMV conducted the fieldwork. MD, MdC and MGG analyzed the data. MD wrote the first draft of the manuscript. All authors contributed to the discussion and revision of the manuscript.

The impact of climate change on the geographical distribution of habitat-forming macroalgae in the Rías Baixas

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Abstract

In the current scenario of climate change characterized by a generalized warming, many species are facing local extinctions in areas with conditions near their thermal tolerance threshold. At present, the southern limit of the geographical distribution of several habitat-forming algae of cold-temperate affinities is located in the Northwest Iberian Peninsula, and the Rías Baixas may be acting as contemporary refugia at the range edge. Therefore, it is necessary to analyze future changes induced by ocean warming in this area that may induce changes in macroalgae populations. The Delft3D-Flow model forced with climatic data was used to calculate July-August sea surface temperature (SST) for the present (1999-2018) and for the far future (2080-2099). Mean daily SST was used to develop and calibrate a mechanistic geographical distribution model based on the thermal survival threshold of two intertidal habitat-forming macroalgae, namely *Himanthalia elongata* (L.) S.F.Gray and *Bifurcaria bifurcata* R. Ross. Results show that *H. elongata* will become extinct in the Rías Baixas by the end of the century, while *B. bifurcata* will persist and may occupy potential free space left by the decline in *H. elongata*.

Keywords: climate change; macroalgae; intertidal organisms; mechanistic species distribution model; Delft3D;CORDEX; CMPI5; RCP8.5

1. Introduction

Ecological systems have to face the modification in environmental conditions that global climate change is causing worldwide (Chen et al., 2011; McMenamin et al., 2008; Parmesan et al., 1999; Poloczanska et al., 2013, 2016). In terrestrial and marine environments, species have to deal with a general increase in warming conditions, which is not spatially homogeneous (Cane et al., 1997). Often, warming results in local extinctions at the low latitude range limits of the species distributions (Russell et al., 2013; Wiens, 2016). Range contraction and local extinction or decrease are especially worrying when affecting habitat-forming species that provide structure, shelter and food to many accompanying species, behaving like ecosystem engineers (*sensu* Jones et al., 1994). The pattern of climate change and, in particular, warming, may be heterogeneous across the latitudinal gradient of a species distribution (Helmuth et al., 2006) and there may be colder favorable spots at the range margins. These cold spots may act as contemporary climatic refugia (Ashcroft, 2010; Keppel et al., 2012), favoring the persistence of edge populations.

Bakun (1990) hypothesized that global warming could strengthen coastal upwelling intensity due to the increase in land-ocean thermal contrast. The strengthening of upwelling-favorable winds would result in cooling of the ocean surface. This hypothesis has been tested for different upwelling systems, finding different trends and concluding that each system responds to global warming differently (Sydeman et al., 2014; Varela et al., 2015; Wang et al., 2015). On the other hand, coastal upwelling regions show lower warming rates than the adjacent ocean (Santos et al., 2012a, b; Bakun et al., 2015; Varela et al., 2018; Seabra et al., 2019). In the same way, the areas affected by river plumes usually show lower warming rates than the

adjacent ocean water (Costoya et al., 2017, 2016). Thereby, coastal upwelling regions, estuaries and adjacent coastal areas may represent climatic refugia for many species.

Coastal rocky systems are among the most productive marine areas (Smale and Wernberg, 2013). In temperate latitudes, these environments are dominated by macroalgae which are declining at a global scale (Kumagai et al., 2018). Kelp forests and the large intertidal macroalgae meadows are threatened in many regions of the planet by climate change, other anthropogenic stressors and local factors (Strain et al., 2014; IPCC, 2015; Krumhansl et al., 2016; Wernberg et al., 2016). The geographical distribution of these species has traditionally been related to water temperature, in addition to other physical factors of regional and local variation, such as marine salinity (reviewed in Lüning, 1990). The southern, lower latitudinal limit of the geographic distribution of several kelps and large intertidal seaweeds is located in the Northwest Iberian Peninsula (NWIP). A marked contraction of the species ranges in this area has been detected in recent years (reviewed in Casado-Amezúa et al., 2019). This is the case of *H. elongata*, which has disappeared from a coastal strip of approximately 130 km since the start of this century in the North Iberian Peninsula (NIP) (Duarte et al., 2013), feasibly due to its restricted thermal tolerance (Martínez et al., 2015). Currently, its distribution is limited to the NWIP corner, including the presence inside the large embayments of the Galician rias and in areas moderately exposed to waves (Martínez et al., 2012). This species exemplifies the decline response observed in other habitat-forming macroalgae of cold-temperate affinities. By contrast, the degree of resilience to warming of other macroalgae with greater tolerance to thermal stress, such as *B. bifurcata*, is still unknown. Currently, the southern limit of *B. bifurcata* is located around upwelling south Morocco regions (Neiva et al., 2015). It helps to explain the *B. bifurcata* shifted southwards in Portugal observed by Lima et al. (2007). Martínez et al.

(2012) projected an increase of its presence in NW Iberia using SST anomalies for the near future (2040). Recent studies indicate that these species of warm-temperate affinity are declining in NIP (Méndez-Sandín and Fernández, 2016). Moreover, models of the whole geographical distribution projected a northward shift of its southern limit and its expansion from its high latitude range limit to Scotland or even Norway (Neiva et al 2015).

Additionally, changes in the distribution of seaweeds could also be related to upwelling variations (Sánchez et al., 2005). The abundance and distribution of seaweeds also depend on important environmental factors, such as exposure to waves and the availability of hard substrate for attachment (Martínez et al., 2012), and anthropogenic factors, as pollution (Fairweather, 1990). It should be noted, that pollution mitigation policies, such as the EU Water Framework Directive (WFD) 2000/60/EC, promoted an improvement in water quality that can lead to a partial recovery of seaweeds communities (Díez et al., 2009, 2012).

The Rías Baixas are four flooded incised valleys (Evans and Prego, 2003) located on the NWIP, at the northern limit of the eastern North Atlantic Upwelling system. They are the southernmost rias of Galicia (Fig. 1). Due to their location, they are strongly influenced by upwelling events. Upwelling, together with other co-varying factors such as the higher water nutrient supply, protection from wave action or river flow (Duarte and Viejo, 2018) may be responsible for the rias to be acting as contemporary refugia to warming (Santos et al., 2011) for large, habitat-forming macroalgae (Lourenço et al., 2016). Although it is expected an intensification of upwelling-favorable winds in the NWIP for the future (Rykaczewski et al., 2015; Sousa et al., 2017), Sousa et al. (2020) have recently shown that coastal upwelling will be less effective due to the increase in the stratification of the upper layer caused by sea surface

warming. In fact, Des et al. (2020) determined that the future increase in water temperature and stratification may negatively affect the growth of *Mytilus galloprovincialis*, the most common species of mussel cultured in the area. Given this previous research, a question immediately arises: will the Rías Baixas act as climatic refugia against seawater warming for large habitat-forming macroalgae in the future?

The aim of this work is to determine how climate change, and SST warming in particular, will affect the geographical distribution of two intertidal macroalgae, *H. elongata* and *B. bifurcata*, within the Rías Baixas. These two species are large, canopy-forming algae that dominate the low intertidal levels of the rocky shores of the eastern Atlantic, which modify the environment and provide shelter and food for a wide variety of organisms (e.g. Niell, 1981; Anadó, 1983; Fernández et al., 1983; Hawkins and Hartnoll, 1985; Gestoso et al., 2010).

Firstly, SST data, computed by means of Delft3D-Flow numerical model, were used to detect heat waves that may affect each of the species. Then, a mechanistic distribution model based on the thermal survival threshold for adult plants of each species was calibrated and used to determine the thermal habitat suitability for the present (1999-2018) and by the end of the century (2080-2099). Thermal survival thresholds for adult plants were previously determined by Martínez et al. (2015).

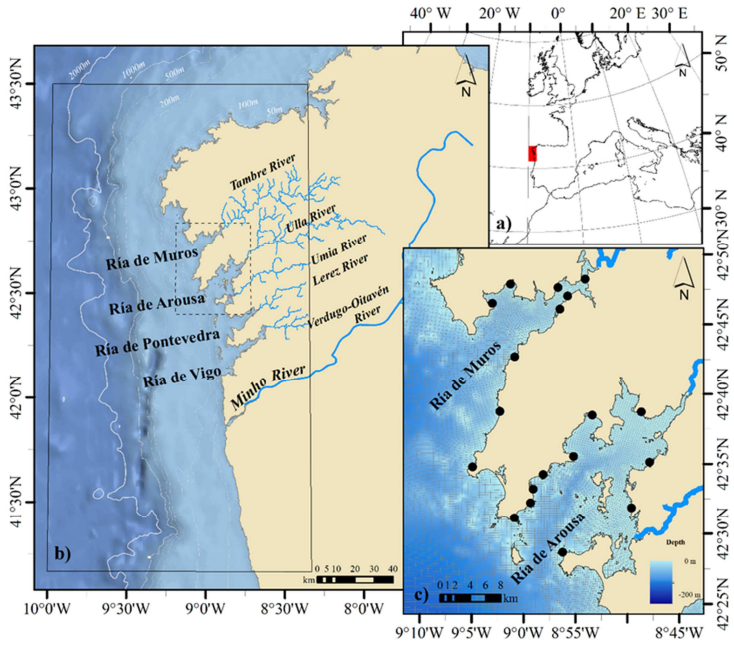

Fig. 1. (a) Location of the study area along the northwestern coast of the Iberian Peninsula. **(b)** The box indicates the modeled area. **(c)** A close-up view of the Ria de Muros and the Ria de Arousa is shown with the numerical grid and the position of TidbiT data loggers sampling stations (black points).

2. Methodology

2.1. Hydrodynamic numerical model

Sea surface temperature (SST) was computed using the hydrodynamic numerical model Delft3D-Flow. Numerical simulations of transport conditions were performed using the mesh, parametrization and implementation previously validated for the Rías Baixas by Des et al. (2019, 2020). The main characteristics of the numerical model configuration are described below; however, for a more detailed description of the parametrization see Des et al. (2019, 2020).

The computational grid covers from 8.33ºW to 10.00ºW and from 41.18ºN to 43.50ºN (Fig. 1b, rectangle). A curvilinear irregular grid was adopted with 452 x 446 cells, and a mean resolution of 2200 m × 800 m on the west boundary, gradually increasing towards onshore, allowing higher resolution in the Rias (220 m x 140 m) and

the Minho estuary (50 m × 77 m). This high spatial resolution allows Delft3D-Flow to provide, among other variables, SST data in the areas of the Rías Baixas that represent the natural habitats for intertidal macroalgae such as *H. elongata* and *B. bifurcata*. The model uses 16 sigma layers with refined surface layers at the surface.

The bathymetric dataset for model simulations was created compiling data from different sources. Multibeam-sourced bathymetry with a resolution of 5 m for the rias of Vigo and Pontevedra was provided by the General Fishing Secretary. The bathymetry of the Ría de Arousa, the Ría de Muros and the adjacent shelf area was obtained from nautical charts of the Spanish Navy Hydrographical Institute. The Minho estuary bathymetry was provided by the Portuguese Navy Hydrographic Institute. Gaps in the dataset were filled using data from the General Bathymetric Chart of the Oceans with a horizontal resolution of 30 arc seconds (GEBCO, https://www.gebco.net/).

The oceanic boundary was forced with transport conditions (salinity and water temperature) and water level. Tidal harmonic constituents (M_2, S_2, N_2, K_2, K_1, O_1, P_1, Q_1, M_{sF}, MM, M_4, MS_4, MN_4) were obtained from the model TPXO 7.2 TOPEX/Poseidon Altimetry (http://volkov.oce.orst.edu/tides/global.html) and were prescribed as astronomical forcing at the oceanic open boundary. River discharges are imposed as fluvial open boundary condition. The exchange of heat through the free surface was simulated using the "absolute flux, net solar radiation" model. This model requires relative humidity, air temperature and the combined net solar (short wave) and net atmospheric (longwave) radiation. The heat loss due to evaporation and convection is computed by the model (Deltares, 2014). Wind components and pressure values are imposed varying spatially.

Following the procedure described by Des et al. (2020), two numerical experiments were performed. In the first one (Exp#1 from now on), Delft3D was mainly

forced with measured and reanalysis data, and the hydrodynamics of the study area was simulated for a historical period. In the second experiment (Exp#2 from now on), the model was mainly forced with historical and future data from the Regional Circulation Models (RCM) driven by General Circulation Models (GCM) executed in the framework of the Coordinated Regional Climate Downscaling Experiment (CORDEX) project (http://www.cordex.org/). Both experiments were run for July and August using a spin-up period of two weeks.

Exp#1 was run for 2012 to be compared with *in situ* coastal temperature data. The thermohaline boundary conditions for Exp#1 were imposed using daily data from the operational Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis (http://marine.copernicus.eu/). Data from MeteoGalicia Weather Research and Forecasting Model (https://www.meteogalicia.gal), were used as surface boundary conditions. Minho River discharge data were provided by the Confederación Hidrográfica Miño-Sil (http://saih.chminosil.es), while Verdugo-Oitavén, Lérez, Ulla, and Umia rivers discharge data were retrieved from the MeteoGalicia database.

Exp#2 was run for the historical (1999 - 2018) and future (2080-2099) periods under climatic conditions to perform geographical distribution maps of *H. elongata* and *B. bifurcata* for the present and the future climate periods. Data for ocean boundary conditions were retrieved from the MOHC-HadGEM2-Es GCM outputs (https://esgf-node.ipsl.upmc.fr/projects/esgf-ipsl/). Surface boundary conditions were obtained from the MOHC-HadGEM2-Es-RCA4 RCM outputs (http://www.cordex.org/). Among the available scenarios, the RCP8.5 greenhouse gas emission scenario was considered for future projections. This scenario is quite likely considering the current increase in greenhouse gas emission (Brown and Caldeira, 2017). Climatologic river discharge data were obtained from the Hype Web portal (https://hypeweb.smhi.se) and a reduction of

25% in river discharge was considered for future projections (https://hypeweb.smhi.se/explore-water/climate-impacts/europe-climate-impacts/).

2.1.1. Validation of the Hydrodynamic numerical model

As stated above, the capability of the hydrodynamic numerical model to reproduce the hydrodynamic conditions of the Rías Baixas was previously assessed and validated by Des et al. (2019, 2020). In addition, further checking of the skill of the numerical model to reproduce water temperature in shallow coastal areas was carried out using temperature data measured *in situ* using 19 TidbiT data loggers (9 located in the Ría de Muros and 10 in the Ría de Arousa, Fig. 1c). Data loggers recorded the temperature every 30 minutes from January 2012 to September 2013, but only temperatures of August 2012 at the time of high tides were used to validate the model. *In situ* water temperature measurements were compared with simulated temperature data using the root mean square error, bias and Pearson product-moment correlation.

The root mean square error (RMSE), bias and Pearson product-moment correlation (r) were calculated as

$$RMSE = \left\{\frac{1}{N}\sum_{i=1}^{N}|X_{obs}(t_i) - X_{mod}(t_i)|^2\right\}^{1/2} \quad (1)$$

$$Bias = \frac{1}{N}\sum_{i=1}^{N}(X_{mod}(t_i) - X_{obs}(t_i)) \quad (2)$$

$$r = \frac{\sum_i (x_{obs}(t_i) - \overline{x_{obs}})(x_{mod}(t_i) - \overline{x_{mod}})}{\sqrt{\Sigma_i (x_{obs}(t_i) - \overline{x_{obs}})^2}\sqrt{\Sigma_i (x_{mod}(t_i) - \overline{x_{mod}})^2}} \quad (3)$$

where $X_{obs}(t_i)$ and $X_{mod}(t_i)$ are the observed (measured *in* situ) and modeled (computed–with Delft3D) water temperature, respectively, and N is the number of samples. Bias and RMSE were averaged in order to obtain a mean value for each station.

208 *2.2. Mechanistic modeling of the geographic distribution of macroalgae*

209 The distribution models were based on the thermal tolerance threshold for the
210 species survival. The water temperature data obtained from the first layer of the
211 hydrodynamic model was considered as the predictive variable because SST is
212 significantly correlated with the distribution of *H. elongata* and *B. bifurcata*, as it
213 happens, in general, for seaweeds (Lüning, 1990; Martínez et al., 2012). The number of
214 days (with a minimum number of 10 consecutive days) during which the daily mean
215 SST was higher than the physiological threshold of the algae was calculated for the
216 coastal areas of the Rías Baixas. For a better understanding, result were expressed as
217 percentage of time both for historical (July-August 1999 - 2018) and future (July-
218 August 2080-2099) periods. The physiological thresholds considered are based on the
219 lethal conditions determined by Martínez et al. (2015) using adult fronds in tank
220 experiments. This lethal conditions occurred when the mean seawater temperature
221 exceeded the specific threshold value of the species, 18 ºC and 24.7 ºC, for *H. elongata*
222 and *B. bifurcata*, respectively, sometime between days 6 and 13 of the experiment
223 (Martínez et al., 2015). To determine the exact value, the analysis based on the thermal
224 stress was carried out for different heat-wave durations ranging from 6 to 13, adopting
225 in the rest of the study the duration of extreme heat waves that provides the best score.

226 The presence/absence of *H. elongata* and *B. bifurcata* on the shore of the Rías
227 Baixas was determined from a field survey carried out in 2005 to model the distribution
228 of these species in the Atlantic Spanish coast (Martínez et al., 2012). A total of 81
229 locations were visited inside Rías Baixas. The locations in Muros and Arousa Rias were
230 revisited again in 2011 to verify if the distribution of algae had changed since 2005.
231 Substrate and wave action are, together with the thermal conditions, the main factors
232 influencing the settlement of *H. elongata* (Martínez et al. 2012). Therefore, those points

where the presence of *H. elongata* is less probable due to the existence of muddy and sandy substrates were discarded from the analysis. This was determined using the geological maps provided by the Spanish Geological and Mining Institute (IGME) and the information from field campaigns. Additionally, those points where the presence of *H. elongata* is less probable due to the significant wave height (https://www.meteogalicia.gal/modelos/) were also discarded. The distributional records of *H. elongata* were used to adjust the mechanistic distribution model. This species was preferred over *B. bifurcata* because shows less prevalence in the study area. As the presence of a stable population depends on the conditions of several years, the map of percentage of time under lethal conditions for July-August 1999-2011 was used to perform the calibration. A percentage of time of approximately 33% was identified as the threshold for the presence of populations, i.e., none of the present populations was found in grid cells with more than 33% of the days under lethal conditions, which are the periods of at least 10 consecutive days of daily mean SST > 18 ºC (see results). This threshold was used to interpret the current (1999-2018) *H. elongata* maps of thermal habitat suitability, and their future (2080-2099) projections. Areas where the time under lethal conditions exceeds the 33% threshold were interpreted as locations of algae absence. For the remaining areas, three levels of habitat thermal suitability were defined: 1) P1 for values between 0 and 11% ([0, 11] %), representing the optimal conditions, far from the lethal threshold, 2) P2 for intermediate values ((11, 22] %), and 3) P3 for values between 22 and 33% ((22, 33] %), that may represent sub-lethal temperature conditions. The same criteria were used to interpret the *B. bifurcata* distribution maps (using a thermal survival threshold of 24.7 ºC, see results).

Favorability maps were made to indicate the likelihood of the presence of suitable conditions for *H. elongata* and/or *B. bifurcata* by comparing the maps of

thermal habitat suitability. The high suitability values (lethal conditions < 33% of the time) in a grid cell implies that *H. elongata* and *B. bifurcata* can be found. This fact was indicated on the map as coexistence. When the suitability values indicate the absence of *H. elongata,* but the presence *B. bifurcata,* this was labeled on the map as *B. bifurcata*. Finally, when the suitability conditions in a grid cell are unfavorable for both algae, it was indicated as none.

3. Results and discussion

3.1. SST validation

Modeled and *in situ* water temperature at 1 m depth for August 2012 were compared by means of the mean bias and RMSE calculated for each TidbiT logger station (Figure 2). The pattern observed is similar in both rias and, in general, the model tends to underestimate *in situ* water temperature along the northern shores of the rias (Fig. 2 blue dots, negative bias). The model tends to overestimate the water temperature in the inner areas (Fig. 2 red dots, positive bias) and the bias is almost zero along the southern shores. The maximum positive, 0.95 ºC, and negative, -1.57 ºC bias observed are quite similar to those obtained by Des et al. (2020), 1.25 ºC and -1.44 ºC, respectively. In general, there are more stations with high bias and RMSE than observed in Des et al. (2019, 2020) where *in situ* vertical profiles are located in deeper areas. These higher errors are likely due to both the location of the loggers in coastal intertidal areas and the limited horizontal resolution of the mesh due to the complex orography of the rias. Following a similar procedure to that developed in de Pablo et al., (2019), the mean Pearson correlation coefficients were calculated for the Ría de Muros (0.82) and for the Ría de Arousa (0.80**).** Both values show a good agreement between observations and model results.

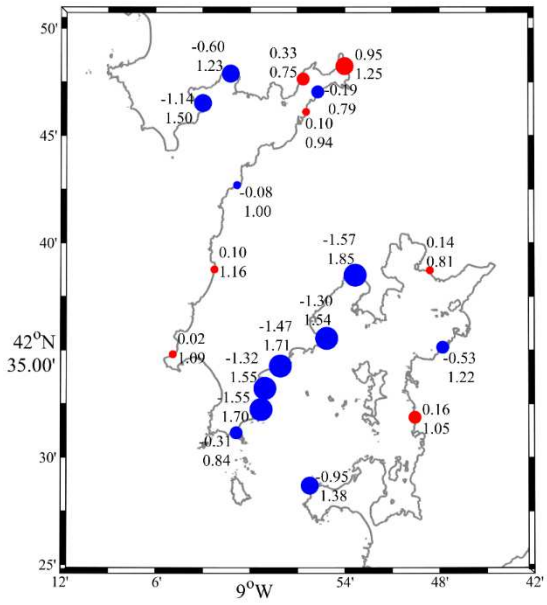

Fig. 2. Mean values of bias (upper number) (ºC) and RMSE (lower number) (ºC) obtained comparing Delft3D-Flow modeled and measured water temperature at 1 m depth for August 2012. Red dots indicate that the model overestimates *in situ* data (positive bias). Blue dots indicate that the model underestimates *in situ* data (negative bias). Dot size indicates the bias percentile.

3.2. Calibration of the species distribution model

Based on the experiments developed in Martínez et al., (2015), where the lethal conditions for *H. elongata* occurred sometime between days 6 and 13 of the experiment, a thermal stress analysis was performed in which several heat-waves were considered with durations between 6 and 13 days. 10-day heat-wave was shown to provide the highest number of presence/absence successes regarding field data and it was considered for further analysis. Additionally, the maximum percentage of time under lethal conditions suffered by any stable population of *H. elongata* for the period 1999-2011 (July-August) was 33%. In this study, this value was observed for the northernmost population located in the inner part of the Ría de Muros (Fig. 3, blue dot). When applying this threshold, the mechanistic models properly classify 18 presences (100% of sensitivity) and 10 absences, providing 13 false presences (Fig. 3, filled

yellow dots located in the cyan area). This is well known limitation of mechanistic distribution models based only on the physiological threshold of the species, which tend to over-predict species prevalence (Martínez et al., 2015). The false presences can be associated to other environmental factors, such as high atmospheric temperatures during low tide affecting those individuals inhabiting the low intertidal, the tidal range or the wind speed (Martínez et al., 2012, de la Hoz et al., 2019). Despite the model tending to over-predict the presence of *H. elongata*, it can provide useful information about potential areas of extinction in the future.

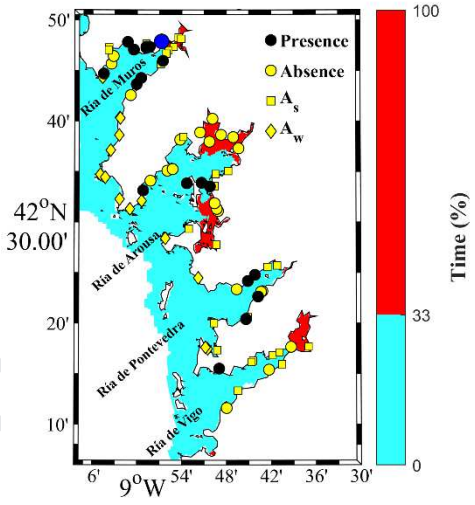

Fig. 3. Percentage of time (July-August 1999-2011) during which *H. elongata* supports lethal conditions. Filled black points indicate the presences. Filled yellow points indicate the absences. Filled yellow squares indicate absences associated with unfavorable substrate or/and unfavorable significant wave height ($Absence_{sw}$). Data recorded in a field survey carried out in 2005 (and re-surveyed in 2011). Filled blue point indicates the location of the presence record which tolerates lethal conditions for more percentage of time. Cyan represent areas suitable for presence and red for absence.

3.3.Maps of thermal habitat suitability

316 The potential effect of SST warming on the geographical distribution of *H.*
317 *elongata* and *B. bifurcata* was estimated comparing the geographical map of thermal
318 habitat suitability for the far future (2080-2099) with the present map (1999-2018).

319 The map of thermal habitat suitability of *H. elongata* for the present (Fig. 4a)
320 shows that the thermal conditions of the Rías Baixas are mostly favorable to the
321 presence of the alga. The inner part of the rias, part from the existence of muddy
322 bottoms and low wave agitation, shows unfavorable thermal conditions since upwelling,
323 which reduces water temperature, is negligible. A more detailed analysis shows that the
324 rias of Muros and Arousa display the most suitable conditions, although the time under
325 lethal conditions increases in the middle part of the Ría de Arousa compared with the
326 outer part. The rias of Pontevedra and Vigo show thermal conditions in the P2 range,
327 indicating that the thermal conditions of these two rias are slightly less favorable than
328 those in the other two northern rias. The records of presence/absence of *H. elongata* and
329 other species of cold-temperate intertidal fucaceae, e.g., *Fucus serratus* (L.), collected
330 during a field survey by Martínez et al. (2012), show a higher presence in the rias of
331 Muros and Arousa than in the rias of Pontevedra and Vigo. These observations support
332 the differences in thermal conditions between the Rías Baixas, since a greater presence
333 was recorded in the rias where thermal conditions are more favorable.

334 Projections for the far future (Fig. 4b) under the RCP 8.5 greenhouse gas
335 emission scenario indicate that thermal conditions in the Rías Baixas will be lethal for
336 *H. elongata*, which implies that this species is projected to disappear. A range
337 contraction of 21% was already estimated for this species by the reduction in its extent
338 of occurrence in the Cantabrian Sea and Portuguese coast between the periods 1980's-
339 1990's to 2013-2016, as part of a general declining trend observed for many cold-
340 temperate fucoids and kelps at its southern range limit in the Iberian Peninsula (Duarte

et al., 2013; Casado-Amezúa et al., 2019). *Himanthalia elongata*, together with other species, was suggested to be included in the red list of endangered species of the Spanish government, a decision supported by the results of this study. Currently, the signs of decline inside the rias are less than elsewhere in the open shore, so it can be considered that they are acting as contemporary refugia to warming for several species (Duarte and Viejo, 2018). In the same way, an important habitat-forming species, the kelp *Laminaria hyperborea* (Gunnerus) Foslie, with an upper lethal threshold of 23 ºC, has also suffered a decline inside the Galician rias (Casado-Amezúa et al., 2019). The decline of temperate macroalgae does not occur locally or regionally, it is becoming evident as global warming proceeds in areas as far as Australia and South Africa (Wernberg et al., 2016, 2013; IPCC, 2019). Therefore, in the case of *H. elongata*, whose tolerance limit (18 ºC) is lower than that of *L. hyperborea* (23 ºC), it can be considered that, the Rías Baixas will no longer be refugia for this species by the end of the century under a RCP8.5 greenhouse gas emission scenario.

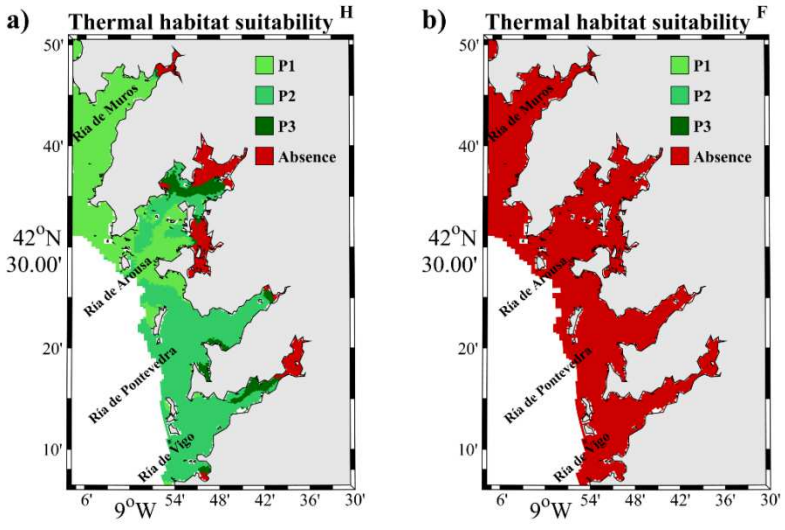

Fig. 4. Thermal habitat suitability for *H. elongata* based on modeled SST for July-August for the present (1999- 2018) (a) and the far future (2080-2099) (b). Green scale represents areas suitable for presence and red for absence. P1 represents optimal conditions, P2 intermediate conditions and P3 sub-lethal SST conditions.

Regarding *B. bifurcata*, whose lethal temperature threshold is higher (24.7°C) than H. *elongata* (18 °C), results for the present (Fig. 5a) show that the thermal conditions of the Rías Baixas are favorable to the presence of the alga. By the end of the century (Fig. 5b), this situation may not vary greatly, and only the innermost part of the rias may turn inappropriate for the algae. As previously stated, the rias are considered contemporary refugia against seawater warming for several species (Duarte and Viejo, 2018) because their tendency towards warming is lower than the trend of adjacent coastal areas. This lower tendency is due to the fact that the rias are located in the northern limit of the eastern North Atlantic Upwelling system which buffers the ocean warming (Santos et al., 2011, 2012ab; Bakun et al., 2015; Varela et al., 2018; Seabra et al., 2019). Thereby, and although the upwelling may be less effective in the future (Sousa et al. 2020), the water temperature within the rias will continue to be lower than at the adjacent coastal areas and, then, they potentially represent climatic refugia for the persistence of *B. bifurcata*, and other species of similar thermal tolerance.

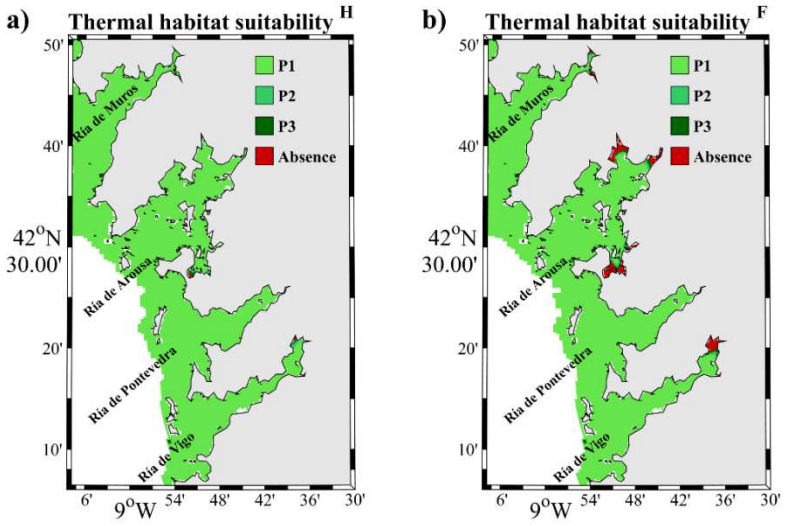

Fig. 5. Thermal habitat suitability for *B. bifurcata* based on modeled SST for July-August for the present (1999- 2018) (a) and the far future (2080-2099) (b). Green scale represents areas suitable for

presence and red for absence. P1 represents optimal conditions, P2 intermediate conditions and P3 sub-optimal and sub-lethal SST conditions.

The upper survival thresholds of other habitat-forming macroalgae are similar to that of *B. bifurcata*. Large intertidal fucoids, namely *Fucus serratus* (L.) and *Ascophyllum nodosum* (L.) Le Jolis, have shown lethal conditions for seawater temperature at about 24 and 25 ºC, respectively. In addition, these species are also influenced by stress during emersion that may act in synergy with seawater warming. The threatened kelp *Laminaria ochroleuca* (Bachelot de la Pylaie, 1824), which is a foundational species known to supports kelp forests in the NW Iberian Peninsula (Voerman et al., 2013), has been shown to die back at 24.6 ºC (Franco et al., 2018). The abundant annual kelp *Saccorhiza polyschides* (Lightfoot) Batters, has an upper survival threshold of 24-25ºC (tom Dieck and de Oliveira, 1993). Arrotes (2002) reported an expansion of *F. serratus* and a contraction of *B. bifurcata* in northern Spain in the 90's, this contrasting pattern was associated with a competitive displacement of the resident species (*B. bifurcata*) by the invasive species (*F. serratus*). Currently, the distribution of these species is suffering a drastic contraction in their extent of occurrence in the Cantabrian Sea and Portuguese coast, as well as local declines in abundance in some populations inside the rias, but most populations currently have found refugia inside the rias (Casado-Amezúa et al., 2019). Thus, we may hypothesize that the water thermal conditions of the Rías Baixas will be favorable for all these species, as exemplified in this study by *B. bifurcata*. Once the thermal conditions are suitable, the distribution of the macroalgae species communities will be linked to other environmental factors, such as substrate, air temperature and significant wave height (Martínez et al., 2012, De la Hoz et al., 2019; Ramos et al., 2020). Moreover, the distribution of the macroalgae will also depended on their dispersal ability.

Favorability maps (Fig. 6) also confirm that by the end of the century (Fig. 6b) the increase in the water temperature of the rias may lead to increased prevalence of *B. bifurcata* or the aforementioned habitat-forming species of similar thermal tolerance such as *Saccorhiza*. Our findings are in accordance with observations by Ramos et al. (2020), who have recorded an increase of *B. bifurcata*, *Cystoseira baccata* (S.G.Gmelin) P.C.Silva, *Caulacanthus ustulatus* (Mert. ex Turner) Kütz. and *Chondracanthus acicularis* (Roth) Fredericq in the Rías Baixas and the decrease of *H. elongata* in Northern Spain.

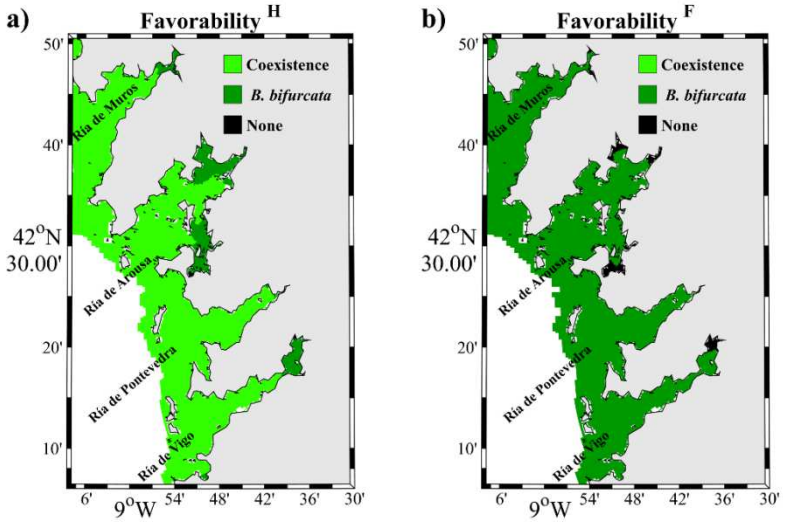

Fig. 6. Favorability maps for *H. elongata* and *B. bifurcata* based on lethal conditions for July-August for the present (1999- 2018) (a) and the far future (2080- 2099) (b). Light green represents the coexistence of both species, dark green the prevalence of B. *bifurcata* and black the absence of both species.

4. Conclusions.

The mechanistic distribution model developed, based on the thermal survival threshold, projects a shift in the macroalgae species communities by the end of the century.

Ocean warming will increase the exposure time of macroalgae to heatwaves, this increase can lead to the local extinction of *H. elongata* and other macroalgae with a similar thermal tolerance.

The analysis of the suitability of the thermal habitat for *B. bifurcata*, whose thermal survival threshold is higher than that of *H. elongata*, shows that thermal conditions by the end of the century can favor the settlement of these macroalgae and other habitat-forming species with a similar thermal tolerance, which makes the Rias Baixas remain as refugia for these species.

Although changes in macroalgal species communities will be led by ocean warming, other environmental parameters should be studied. A downscaling of air temperature projections and numerical simulations of wave height inside the rias could contribute to project shifts in the macroalgae species communities more accurately. Furthermore, the developed model can be used to evaluate possible changes in distribution when evaluating different climate change scenarios, as well as for the near future.

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Highlights

- Climate change impact on habitat-forming macroalgae using numerical predictions
- Ocean warming will increase the exposure time to heatwaves of macroalgae
- *H. elongata* and similar thermal tolerance macroalgae may become extinct locally
- *B. bifurcata* and similar thermal tolerance macroalgae settlements will be favored
- The Rias Baixas will remain as refugia for many species

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: