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Integrating reproductive phenology in ecological niche models changed the predicted future ranges of a marine invader

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Abstract

Aim: Phenology of a wide diversity of organisms has a dependency on climate, usually with reproductive periods beginning earlier in the year and lasting longer at lower latitudes. Temperature and day length are known environmental drivers of the reproductive timing of many species. Hence, reproductive phenology is sensitive to warming and is important to be considered for reliable predictions of species distributions. This is particularly relevant for rapidly spreading non-indigenous species (NIS). In this study, we forecast the future ranges of a NIS, the seaweed *Sargassum muticum*, including its reproductive phenology.

Location: Coastal areas of the Northern Hemisphere (Pacific and Atlantic oceans).

Methods: We used ecological niche modelling to predict the distribution of *S. muticum* under two scenarios forecasting limited (RCP 2.6) and severe (RCP 8.5) future climate changes. We then refined our predictions with a hybrid model using sea surface temperature constraints on reproductive phenology.

Results: Under the most severe climate change scenario, we predicted northward expansions which may have significant ecological consequences for subarctic coastal ecosystems. However, in lower latitudes, habitats currently occupied by *S. muticum* will no longer be suitable, creating opportunities for substantial community changes. The temperature constraints imposed by the reproductive window were shown to restrict the modelled future species expansion strongly. Under the RCP 8.5 scenario, the total range area was expected to increase by 61.75% by 2100, but only by 1.63% when the reproductive temperature window was considered.

Main conclusions: Altogether these results exemplify the need to integrate phenology better to improve the prediction of future distributional shifts at local and regional scales.

KEYWORDS

climate change, invasive species, marine alga, phenology, *Sargassum muticum*, species distribution models

*Equal contribution.

1 | INTRODUCTION

New environmental conditions resulting from climate changes are expected to result in shifts of species distributions and abundances, and this raises particular concerns for expansion of non-indigenous species (NIS) (Bates et al., 2014). Climate change may benefit NIS by increasing their abundance and/or accelerating range expansions (Hellmann, Byers, Bierwagen, & Dukes, 2008; Rahel & Olden, 2008). Such changes can potentially impact both diversity and functioning of ecosystems (Edwards & Richardson, 2004). Among the factors shaping species ranges (i.e., abiotic, biotic, dispersal strategies and capacity to adapt to new conditions; Soberon & Peterson, 2005), temperature is believed to be one of the most important (Eggert, 2012; Hoek, 1982; Lüning, 1990). In marine macroalgae (i.e., seaweeds), temperature affects individual performance (i.e., photosynthesis, growth and reproduction) and determines tolerance or survival limits (Breeman, 1990; Eggert, 2012). Quoting Breeman (1990), northern boundaries of seaweed ranges are established “by low lethal winter temperatures, or by summer temperatures too low for growth and/or reproduction,” while southern boundaries are established “by high lethal summer temperatures, or by winter temperatures too high for induction of a crucial step in the life cycle.” These thermal thresholds are commonly related to the tolerance of the hardest life history stage (e.g., microthallus development), and temperature requirements for reproduction and growth (Breeman, 1990). Seaweeds are thus particularly sensitive to the cumulative effect of changing temperatures and their distributional range is expected to be strongly impacted by climate change. Warming may favour opportunistic and tolerant seaweeds by increasing their competitive ability (Dukes, 2007). Substantial changes of seaweed species ranges, including NIS, are thus expected and predicted as a response to changing seawater temperature (Assis, Serrao, Claro, Perrin, & Pearson, 2014; Breeman, 1990; Neiva et al., 2015).

In this context, ecological niche models (ENMs, i.e., species distribution models/habitat suitability models) have been increasingly used in support of invasion biology studies (Barbosa, Schneck, & Melo, 2012; Jiménez-Valverde et al., 2011). Seaweeds are no exceptions and ENMs have been used to assess the likelihood of establishment success in a novel area, identify critical routes and arrival points, and forecast range expansions and contractions under climate change (e.g., Verbruggen et al., 2013, 2009; Marcelino & Verbruggen, 2015; Chefaoui & Varela-Álvarez, 2018). Most ENMs are based on a correlative approach between species occurrence or abundance data with environmental factors and/or spatial characteristics, yielding maps of habitat suitability or probability of presence (Chefaoui, Casado-Amezúa, & Templado, 2017; Elith & Leathwick, 2009; Guisan & Thuiller, 2005). Among the challenges faced when using ENMs for studying NIS, the integration of physiological data, notably to better integrate phenology in ENMs, is critical for getting more robust predictions (Kearney & Porter, 2009; Marcelino & Verbruggen, 2015).

Integrating phenological trends would facilitate the assessment of species' sensitivity to climate change and improve the prediction of future distributional shifts at local and regional scales (Chuine,

2010; Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Diez et al., 2012). Shifts in reproductive phenology (i.e., variations in timing and length of reproductive seasons) are among the primary responses of organisms to climate change (Dunn, 2004; Edwards & Richardson, 2004; Menzel et al., 2006; Parmesan & Yohe, 2003; Poloczanska et al., 2016). Earlier and longer warm seasons may lead to a prolonged period of reproduction and may subsequently impact demography and population dynamics (Edwards & Richardson, 2004; Miller-Rushing, Hoyer, Inouye, & Post, 2010; Poloczanska et al., 2016). These climate change-induced shifts in reproductive phenology may thus in turn alter community-level patterns, affecting competition and reshaping assemblages (Post, Forchhammer, Stenseth, & Callaghan, 2001; Sherry et al., 2007; Waser & Real, 1979). Nevertheless, most studies aimed at understanding seasonal phenological shifts in relation to climate were conducted on terrestrial species (Chuine, 2010; Parmesan & Yohe, 2003; Walther et al., 2002), with a limited number on aquatic species (Burrows et al., 2011; Thackeray et al., 2010) including invasive ones (Wolkovich & Cleland, 2011).

As highlighted above, temperature is a major driver of distributional ranges in marine seaweeds (Breeman, 1990; Eggert, 2012). Seaweed phenology, particularly the timing and duration of the reproductive period, is strongly influenced by temperature (Breeman, 1988; Deysher, 1984). In the case of NIS, this dependency of reproductive timing on temperature might impose an additional constraint for their persistence once a new region has been colonized, which could limit the expansion of NIS in the invaded range. Day length is an additional important factor that affects reproductive timing in seaweeds (Breeman, 1993; Cunningham, Guiry, & Breeman, 1993; Voskoboinikov, Breeman, Hoek, Makarov, & Shoshina, 1996) and notably the maturation of reproductive structures in *S. muticum* (Strong, 2003). For instance, based on an individual-based model of population growth of the invasive kelp *Undaria pinnatifida*, Murphy, Johnson, and Viard (2016) showed that the fertility of gametophytes is negatively correlated with day length, suggesting that gametogenesis is mostly occurring during the shorter days of winter. Differences in recruitment patterns between the northern and southern range colonized by this NIS were also explained by different responses of the different life cycle stages to both suboptimal temperature and irradiance conditions (Murphy, Johnson, & Viard, 2017). Life cycle and reproduction of many marine species are a cumulative and combined response to temperature, day length and irradiance.

In this context, the invasive brown seaweed *Sargassum muticum*, native to Asia, is particularly interesting to examine. Its presence outside its native range was first reported in the 1940s, along the Pacific Coast of North America. Another major event of introduction later occurred in the 1970s along the North Atlantic coast of Europe (Engelen et al., 2015). Among the 346 introduced seaweeds reported so far at a worldwide scale (Thomsen, Wernberg, South, & Schiel, 2016), *S. muticum* can be considered one of the most successful invaders. As such, it has been the focus of numerous studies. It nowadays displays a very large distribution range, spanning from Mexico to Alaska in America, and from Morocco to Norway

in Europe. This pseudo-perennial species thus expanded its range over extended latitudinal ranges, in less than 40 years in Europe. In addition, diverse consequences on native species and ecosystems have been documented (e.g., Eno, Sanderson, & Conservation, 1997; Britton-Simmons, 2004; Salvaterra, Green, Crowe, & O'Gorman, 2013; DeAmicis & Foggo, 2015). For instance, *S. muticum* can increase biodiversity in areas where macrophytes are not present yet. In other places, it was shown to alter native ecosystem function and structure. Considering the diverse impacts documented so far, it is important to ascertain whether the current distribution is likely to continue to expand or might contract under future climate change.

Presently, *S. muticum* is probably close to its distributional equilibrium with the environment since it has likely invaded a large representation of its suitable sea surface temperature in the Northern Hemisphere; thus, reducing uncertainty in niche models (Jiménez-Valverde et al., 2011). In addition, it is noteworthy that, although the information mainly comes from local studies, the species seems to display latitudinal phenological variations and acclimation to a large range of environments (see references in Engelen et al., 2015). In this study, we use ecological niche modelling to predict the future range, and thus the invasion dynamics of *S. muticum*, but we do so with an innovative approach by accounting for reproductive phenology. The species can reproduce only via sexual reproduction, and it is self-compatible hermaphroditic. Fertilization is external but the zygote remains attached to the apical reproductive structures (receptacles) for 1–3 days after fertilization while initiating embryonic development. The embryos usually sink and settle immediately below or within a few meters of the maternal individual. However, a modelling approach suggested that kilometre-scale dispersal can also occur for 10%–20% of embryos under moderate current speed (Gaylord, Reed, Raimondi, Washburn, & McLean, 2002). In addition, another way to disperse is through drifting thalli. Drifting thalli cannot reattach to solid substrata or to other algae but, when carrying fertilized eggs, they can provide recruits via sexual reproduction while floating (Fletcher & Fletcher, 1975; Norton, 1977). Thus, in theory the species could colonize areas outside its reproductive window, through sexually reproducing drifting thalli, or embryos kept in suspension by turbulence. In addition, this NIS can also be dispersed by human actions, as during colonization of Europe by propagules attached to oysters. Given its high dispersal potential and semi-perennial life history (living from few years up to perhaps decades, under very favourable conditions), some populations colonizing the edge of its distribution might not be able to reproduce and release propagules. Thus, we hypothesize that the correlative models would overestimate the future habitat for the species at the edge of its distribution, where the species could colonize and grow but never reproduce. We use reproductive windows associated with sea surface temperature and day length along the latitudinal gradient of the distribution to produce more reliable forecasts, under the assumption of conservatism of niche and reproductive physiological constraints over time. Thus, we produce a hybrid model combining species range forecasts with abiotic constraints associated with the reproductive phenology of the species. We hypothesize this approach will reduce

overprediction of the future invaded range, by identifying the habitats where the NIS will not persist for generations due to reproductive limitations. To our knowledge, this study is the first to include phenological data in ENMs to improve predictions of seaweed invasion dynamics under scenarios of climate change.

2 | METHODS

2.1 | Biological data and study area

The entire known distribution range of *S. muticum* in the Northern Hemisphere was considered in the models, thus including occurrence data from both the native (Asia) and introduction ranges (North America and Europe). *S. muticum* presence records were obtained from the literature and online databases, including the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>), Ocean Biogeographic Information System (OBIS; www.iobis.org), and *S. muticum* distribution records in Europe of the Ghent University Phycology Lab (<http://www.phycology.ugent.be/research/invasives/map.html>; Engelen et al., 2015). The occurrences were reviewed to correct or exclude those with referencing errors (e.g., records on land belonging to herbaria data). From the determined geographic extent, cells ranging from 0 to 30 m depth were selected, as the maximum depth at which attached *S. muticum* is found along the coastline. Delimiting a depth threshold for the study area was implemented using the 30 arc-seconds resolution bathymetric data derived from the General Bathymetric Chart of the Oceans (GEBCO) website (<http://www.gebco.net/>). For georeferencing of *S. muticum* occurrence data and environmental variables, a resolution of 5 arc minutes (~9.2 km at the equator, 2.4 km at 60°N) was applied. In total, 2,587 *S. muticum* occurrence records were obtained, which corresponded to 1,115 presence cells (Asia: 65; N. America: 185; Europe: 865). The database of occurrence records compiled for *S. muticum* is available in Supporting Information Appendix S1 and Figure 1.

2.2 | Environmental data

The initial set of environmental variables for present climate conditions included the monthly average of (a) sea surface temperature (SST maximum, mean, minimum and range), and surface air temperature (SAT max., mean, min. and range), and (b) salinity. Note that SST changes have been pointed as a good indicator of climate change and its impact on phenology in marine systems (Edwards & Richardson, 2004). Surface air temperature was selected as predictor for *S. muticum* since the NIS can be also present on the low-intertidal shore (see e.g., Andrew & Viejo, 1998). Salinity can be also influential as the initial life stages of *S. muticum* can be less tolerant to brackish water (Steen, 2004). The data were derived from the Bio-ORACLE dataset (Tyberghein et al., 2012) and tested by Pearson's correlation coefficient $<|0.86|$ in the study area. Multi-model ensembles were calculated based on five Ocean General Circulation Models (CNRM-CM5, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-MR and NASA/GISS) belonging to the Coupled Model Intercomparison Project

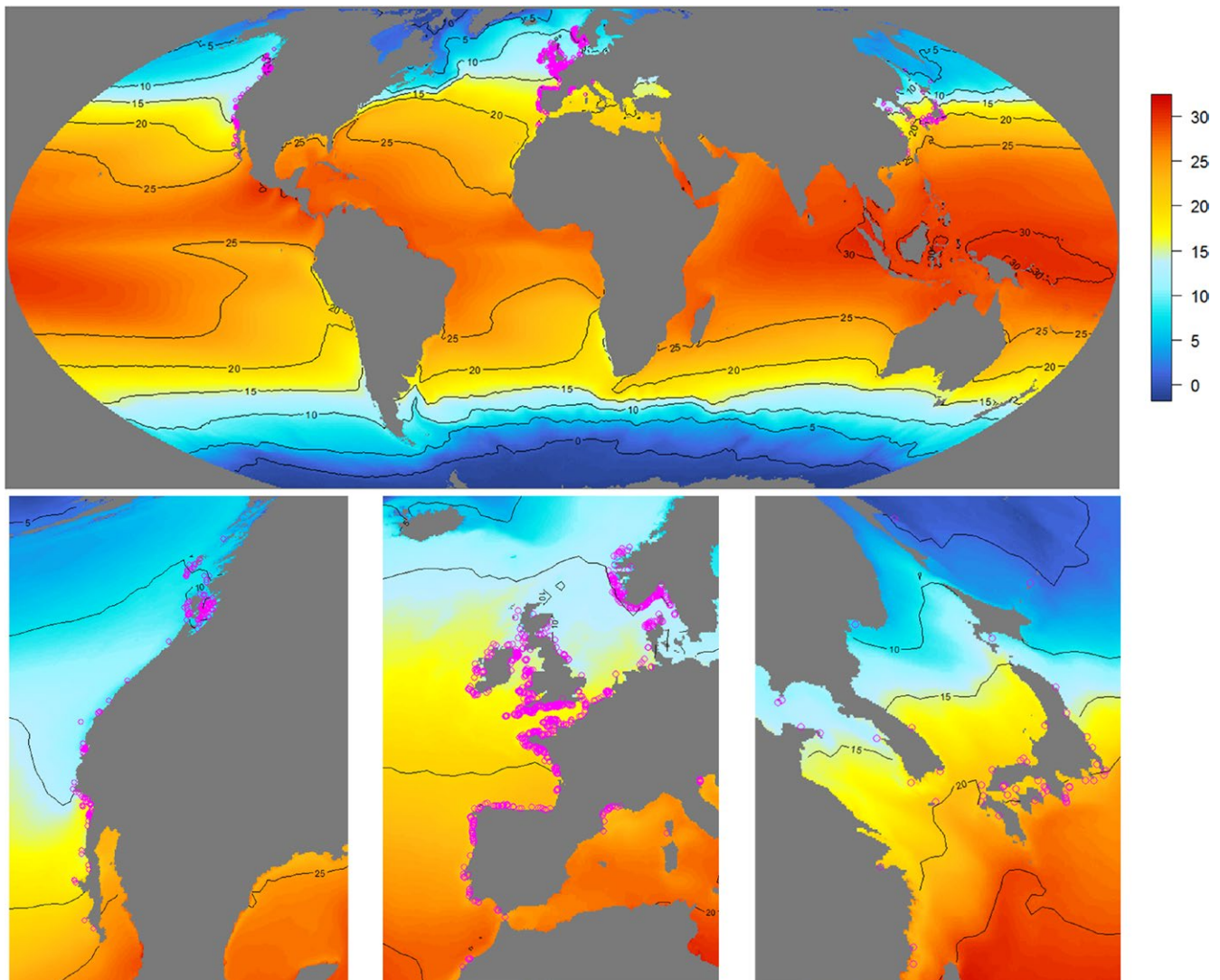


FIGURE 1 Records of *Sargassum muticum* included in the current analysis (magenta points) showing its distribution in the Northern Hemisphere along its native range in Asia (right) and invaded European (middle) and North American (left) ranges. Only 10% of occurrences were outside the mean sea surface temperature threshold found in the literature for the reproductive window

Phase 5 (CMIP5; <http://cmip-pcmdi.llnl.gov/cmip5/>). To project the future distribution of *S. muticum*, ensembles were generated for two extreme future conditions by 2050 (from 2030 to 2050) and 2100 (from 2080 to 2100) with RCP (Representative Concentration Pathways) 2.6 representing the low greenhouse gas emissions scenario and RCP 8.5 as the most pessimistic scenario according to the Intergovernmental Panel on Climate Change—IPCC (Moss et al., 2010; Van Vuuren, Edmonds, Kainuma, Riahi, & Weyant, 2011).

2.3 | Current and future species distribution models

First, we tested if the NIS was close to its distributional equilibrium with the environment in the Northern Hemisphere. We compared the range of environmental values recorded for locations of occurrence of the species within its native range (Asia), with the range of environmental values recorded in the invaded regions (Europe and North America).

To obtain the current and future climate scenarios' predictions for the distribution of *S. muticum*, an ensemble approach was applied. We used pooled datasets (occurrences from the native and invaded ranges) to train the models as this practice enhances the reliability of NIS predictions (Broennimann & Guisan, 2008; Chefaoui & Varela-Álvarez, 2018; Jiménez-Valverde et al., 2011). The “biomod2” package (Thuiller, Georges, Engler, & Breiner, 2016) was used to fit six presence–absence modelling algorithms: flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS) and randomForest (RF). We used an equal number of pseudo-absences extracted at random as presence cells (Lobo, 2008). All models were implemented using the “biomod2” package in R (Thuiller et al., 2016). We ran five iterations for each modelling technique, thus, 30 models for each time and scenario were generated to produce the corresponding ensembles. The data were split into

a calibration (70%) and a validation set (30%) in each of the five iterations performed for each model. The models' performance was assessed using the true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006), the receiver operating characteristic (ROC) curve (AUC), as well as ROC derived sensitivity and specificity (Fielding & Bell, 1997). To evaluate the predictive models, a set of thresholds was tested, and the threshold which optimized the AUC and TSS scores was chosen (Thuiller et al., 2016).

The final prediction under current conditions represented an ensemble calculated through the average of binary predictions (committee averaging ensemble), which was previously demonstrated to have the best performance in predicting coastal species distribution (Chefaoui, Assis, Duarte, & Serrão, 2016). To produce the ensemble, only the models which obtained TSS >0.8 were used. To project the future distribution of *S. muticum*, ensembles were projected to the RCP 2.6 and RCP 8.5 scenarios by 2050 and 2100. To assess the uncertainty of future projections, a clamping mask was generated. The clamping mask compared the values of the variables between the training range and the future scenarios, to identify the regions where the extrapolation of models can happen. The importance of each variable was assessed using a procedure similar to "random-forest" (Liaw & Wiener, 2002). A relative importance value from 0 to 1 (with one being of highest importance) was obtained for each variable by the correlation between the full model and a model rearranged without the examined variable using three iterations (Thuiller et al., 2016).

2.4 | Hybrid model

We retrieved from the literature data on the reproductive window of *S. muticum*, to refine our future projections. From the 36 revised studies, only five provided SST data that could be used to reach our objectives (Supporting Information Appendix S2). These five local-scale studies examined fertility in *S. muticum* populations located in: (a) California and Washington (USA; Deysher, 1984; Norton & Deysher, 1989); (b) Portsmouth (UK) and Tsuyazaki (Japan) (Deysher, 1984); (c) the Baja California peninsula (Mexico; Espinoza-Avalos, 1990); and (d) Luanco (Spain; Arenas & Fernández, 1998; Fernández, 1999).

Our initial intention was to incorporate tolerances on both SST and day length. Thus, we estimated the mean monthly day length at the coldest and warmest months of the reproductive window found by the five studies referred above. We used the NOAA Solar Calculator (<https://www.esrl.noaa.gov/gmd/grad/solcalc/>) to estimate the day length during the reproductive window at the locations of the studied sites. We found that the day length reproductive window ranged from 10 hr 48 min to 15 hr 54 min (Supporting Information Appendix S2). Then, we calculated the days of the year (ranging from 0 to 365) with light within the thresholds in the entire study area (latitude 8°–70°) using the "geosphere" package in R. At the northernmost latitude (70°), we found day length within the thresholds from day 70 to 104, and from day 243 to 277. For the southernmost limit (latitude 8°), this day length threshold can

be found throughout the year. Given the large range found, we concluded the day length reproductive window does not seem to be a limitation for the species persistence, thus we did not use any filter for the predictions related to day length.

For the SST window, we retrieved the minimum and maximum values of monthly mean SST of the warmest and coldest months within the *S. muticum* reproductive window (Supporting Information Appendix S2). Based on the data collected, the reproductive SST window of *S. muticum* was found to be large, ranging from 10°C to 27°C. We applied these thresholds to reclassify the ensembles of mean SST pertaining to each RCP scenario by 2050 and 2100 using the "raster" package in R. Finally, we only used the mean SST related to the reproductive window of *S. muticum* to filter the predictions obtained by the correlative species distribution models. We applied the true skill statistic (TSS) related threshold to transform predictions of the correlative and hybrid models into binary maps. We estimated the change in suitable habitat through the various predictions as a percentage of cells.

3 | RESULTS

3.1 | Species distribution models

Following the Pearson correlation analysis results, three variables were used in the ecological niche models (ENMs): maximum SST, minimum SST and salinity. The ranges defined by the native and invasive occurrences were quite similar for the SST but differed for the salinity. The thermal thresholds (the lowest value of Min. SST and the highest value of Max. SST) of the records of the invaded ranges were within those of the native range, but the NIS showed wider ranges of salinity in the invaded regions (Figure 2 and Table S3.1 in Supporting Information Appendix S3).

Overall, the validation scores for the models of *S. muticum* were high (Tables 1 and S3.2 in Supporting Information Appendix S3). The generalized boosting model (GBM) and Random Forest (RF) were the most accurate, obtaining the highest validation scores with TSS = 0.859 (Table 1). The lowest validation scores were produced by the generalized additive model (GAM) with TSS = 0.828 (Table 1). Maximum sea surface temperature was the variable with the highest relative importance (SST max. = 0.77) for the ensemble model, compared to the minimum sea surface temperature (SST min. = 0.45) and salinity ($S = 0.21$). This suggests that the maximum SST may act as a limiting factor of the current distribution of *S. muticum* in the southern limit. Salinity seems to have the least effect on the distribution model since most of the study area shows values within the tolerance range of the species (see Figure 2). However, its inclusion might have reduced the predicted probabilities of occurrence in the brackish waters of the Baltic Sea or within large reservoirs with fluvial runoff.

Under future climate scenarios, a northward shift in the distribution of *S. muticum*, compared to the current range, was predicted even under the least changing scenario (RCP 2.6 by 2050) (Figures 3 and S3.1 in Supporting Information Appendix S3). In the native range (Japan and adjacent coasts), the highest probability for the future

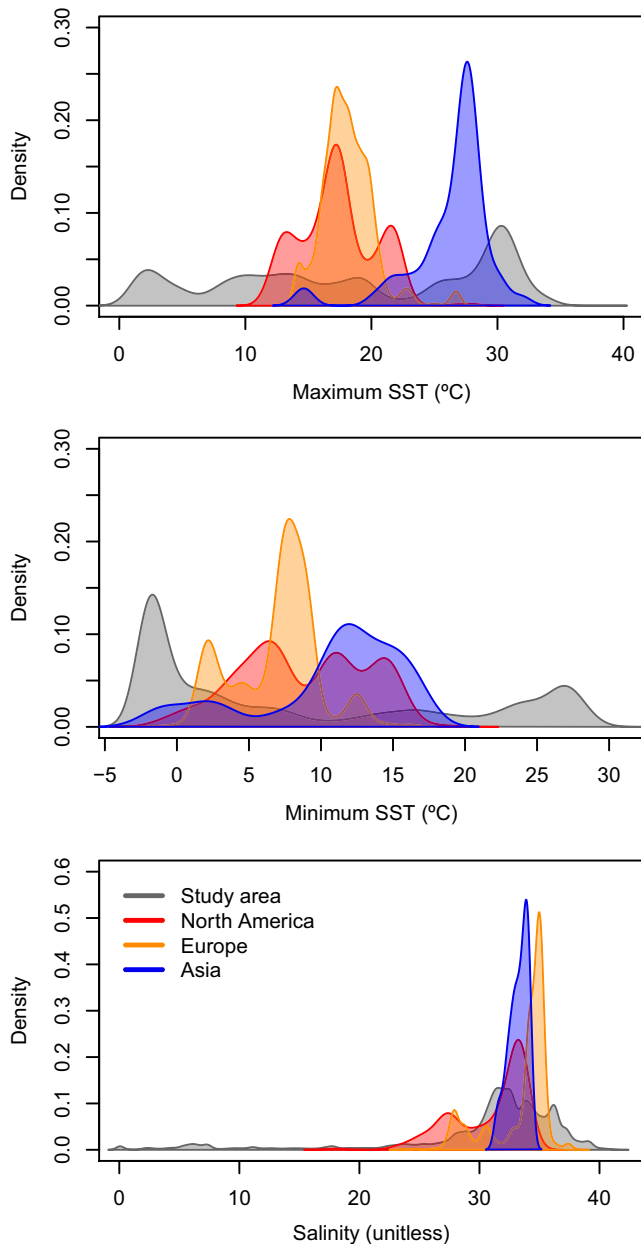


FIGURE 2 Kernel density plots relating the conditions found in occurrence cells of *Sargassum muticum* within its native (Asia) and invaded ranges (North America and Europe) with the study area (the Northern Hemisphere). The ranges of sea surface temperature (SST) were quite similar in the native and invasive occurrences. However, *S. muticum* showed wider ranges of salinity in the invaded regions

S. muticum distribution was northwards from Vladivostok in Russia, Central and Southern Sakhalin, Hokkaido and the entire chain of the Kuril Islands up to Kamchatka. Along the West coast of North America, a substantial northward shift is projected with a complete retreat from Baja California. The highest probability for the species coincided with its current presence along the coast of the US Washington state and British Columbia, while a lower probability is predicted along the coast of Alaska (the Gulf of Alaska; Figure S3.1 in Supporting Information Appendix S3). In addition, substantial

potential colonization (i.e., suitable conditions if the species is introduced) was projected along the US East Coast, including from the Chesapeake Bay northwards along the coast of New England to Nova Scotia and Newfoundland, and up to the southern coast of Hudson Bay (Figure S3.1 in Supporting Information Appendix S3). In Europe, the most probable future distribution of *S. muticum* also coincided with its current distribution in the South-Western fiords of Norway, down to UK, Danish, Dutch, Belgian, French, Spanish and Portuguese coastlines (Figure S3.1 in Supporting Information Appendix S3). However, substantial colonization was also projected in Azores, Mediterranean Sea (along the Southern French, Northern Italian and Croatian coastlines) and the Black Sea. Overall, the relative area increase by 2050 under RCP 2.6, compared to the current distribution, is expected to constitute 51.48% (Figure 4, Figure S3.1 in Supporting Information Appendix S3).

In the most extreme future scenario (RCP 8.5 by 2100), *S. muticum* was expected to show an even more pronounced northward shift. In the native range, the distribution of *S. muticum* is predicted to shift from Chinese and Korean shorelines northwards to the Russian Coast in the Japanese Sea, the Sakhalin Island, Kamchatka and the Kuril Islands (Figure 3). Future distribution along the coast of North America was projected to spread extensively along the Gulf of Alaska (with a lower probability of presence in the Islands of Alaska in the Bering Sea). Our model also projected suitable coasts along the East Coast of US and Canada (extending up to Newfoundland on the East and the Southern Coast of the Hudson Bay on the North), in case the species arrives there (Figure 3). In Europe, future projections indicate that *S. muticum* could be distributed from the Azores to the Faroe Islands, and along the Mediterranean Sea up to the Croatian coast and the Black Sea (Figure 3). There is a lower probability of *S. muticum* spreading in Southeastern Iceland, North-Western fjords of Norway and along the Russian coastline in the Barents and Kara Seas. The total area increased by 2100 under RCP 8.5 is expected to constitute 61.75%, compared to the current distribution (Figure 4). Overall, the area of persistence of *S. muticum* between the present and 2100 (RCP 8.5) was 65.14%. The persistence across time was higher in the invaded regions than in the native area.

The uncertainty in future predictions for both scenarios according to the clamping masks is presented in Figure S3.2 of the Supporting Information Appendix S3. The only areas with uncertainty due to one variable of the future scenarios presenting values outside the range of the current conditions corresponded to the eastern part of the Canadian Archipelago, located north of Hudson Bay (for both RCP scenarios), as well as the areas along the Barents and Kara Seas (for the RCP 8.5 scenario). However, these regions showing uncertainty do not coincide with the predicted areas with high probability of occurrence found by our models.

3.2 | Hybrid model

The records of the NIS match closely the mean SST upper limit corresponding to the suitable reproductive period found in the review of the literature (27°C). For the mean SST lower limit, 10% of all

Model	AUC (\pm SD)	TSS (\pm SD)	Sensitivity (\pm SD)	Specificity (\pm SD)
GLM	0.962 (\pm 0.005)	0.831 (\pm 0.018)	94.328 (\pm 3.364)	88.557 (\pm 2.319)
GBM	0.969 (\pm 0.005)	0.859 (\pm 0.020)	96.194 (\pm 1.275)	90.075 (\pm 2.045)
GAM	0.960 (\pm 0.006)	0.828 (\pm 0.012)	93.731 (\pm 3.403)	88.806 (\pm 2.763)
FDA	0.964 (\pm 0.006)	0.831 (\pm 0.021)	94.179 (\pm 1.055)	90.896 (\pm 1.056)
MARS	0.963 (\pm 0.007)	0.832 (\pm 0.015)	94.627 (\pm 2.254)	87.861 (\pm 3.005)
RF	0.970 (\pm 0.006)	0.859 (\pm 0.021)	94.328 (\pm 0.000)	91.045 (\pm 0.000)

Note. AUC: the area under the curve of the receiver operating characteristic (ROC) curve; TSS: true skill statistic.

TABLE 1 Average validation scores of models obtained for each algorithm: Generalized linear model (GLM); generalized boosting model (GMB), generalized additive model (GAM), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS) and RandomForest (RF)

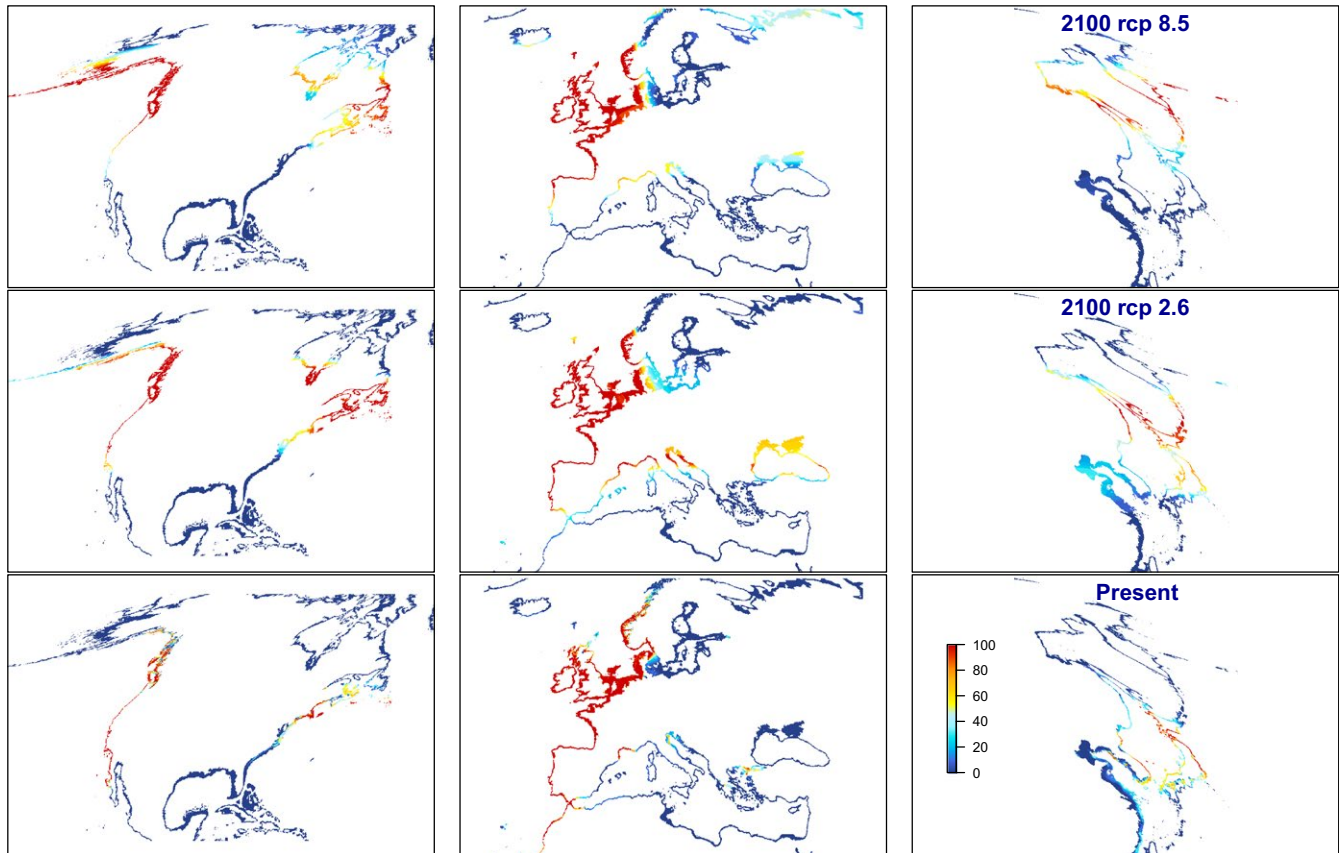
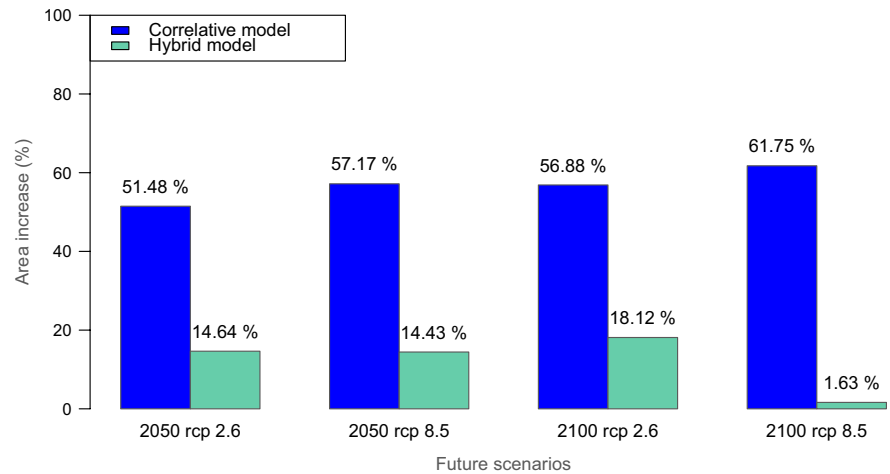


FIGURE 3 Estimated probability of occurrence for *Sargassum muticum* in North America (left), Europe (middle) and its native range in Asia (right), predicted under present conditions and two future scenarios by 2100 (RCP 2.6 and 8.5). A northward shift in the distribution of *S. muticum* is predicted

the records were located below the threshold of 10°C: 7% of the records in Asia, 8% in Europe, and 20% in N. America (see Figure 1 and Table S3.1 in Supporting Information Appendix S3). We overlaid the areas showing future temperatures outside the mean SST threshold for the reproductive window (from 10 to 27°C) on the ensembles for the future by 2100 (Figure 5) and 2050 (Figure S3.3 in Supporting Information Appendix S3). After applying the reproductive phenological information related to the SST, the hybrid models showed a substantial decrease of suitable habitats in comparison with the correlative models (Figure 4). The highest difference was found by 2100 (RCP 8.5), the hybrid model predicted an increase of only 1.63% of the distribution range as compared to

the current distribution (in contrast with a 61.75% increase predicted by the correlative model, Figure 4). The restrictions imposed by the reproductive SST window by 2100 (RCP 8.5) affect mainly the North American (the Bering Sea, northern Gulf of Alaska and the southern Labrador Peninsula) and Asian regions (the Sakhalin Island, Kamchatka and the northern Kuril Islands) (Figure 5). The hybrid models for the remaining scenarios -by 2100 (RCP 2.6) and by 2050- are alike in the latitudinal range covered (see Figures 5 and S3.3 in Supporting Information Appendix S3). They affect the European region (the Norwegian and Scottish coasts of the North Sea), and similar regions in North America and Asia as in 2100 (RCP 8.5), but with the isotherm of 10°C located southwards.

FIGURE 4 Expansion dynamics of *Sargassum muticum*: substantial differences in extension of suitable habitat were found between the correlative and hybrid models. Relative increase of the distribution range between the present and future scenarios was calculated as the number of cells found for each prediction, once applied the true skill statistic (TSS) related threshold to transform predictions into binary maps



4 | DISCUSSION

In this study, we predicted the future distributional dynamics of *Sargassum muticum* in its current native and introduction ranges, integrating correlative ecological niche modelling with critical thresholds for phenology, using data documenting the reproductive period. This study demonstrated the importance of accounting for the physiological limits of essential processes in the life history. Our approach differentiated between the habitats with suitable conditions for the occurrence of the NIS, and the regions where the species is able to reproduce and persist over generations. At higher latitudes, the lower thermal limits observed for growth and survival differ from

those for reproductive success. Under climate change, the northward expansion of this invader would be restricted by the limitation in reproduction imposed by low temperature (for instance due to the inability to develop receptacles). Hence, the hybrid models strongly restricted the future predictions obtained with the correlative species distribution models at the leading edge of the northward range expansion. Under the most severe scenario (RCP 8.5), the prediction for 2100 showed a substantial retreat of *S. muticum* from the southernmost regions of its current range and an important northward shift of its distribution. However, when filtered with the SST delimiting the reproductive window of *S. muticum*, the hybrid model demonstrates that the overall northward increase in distribution

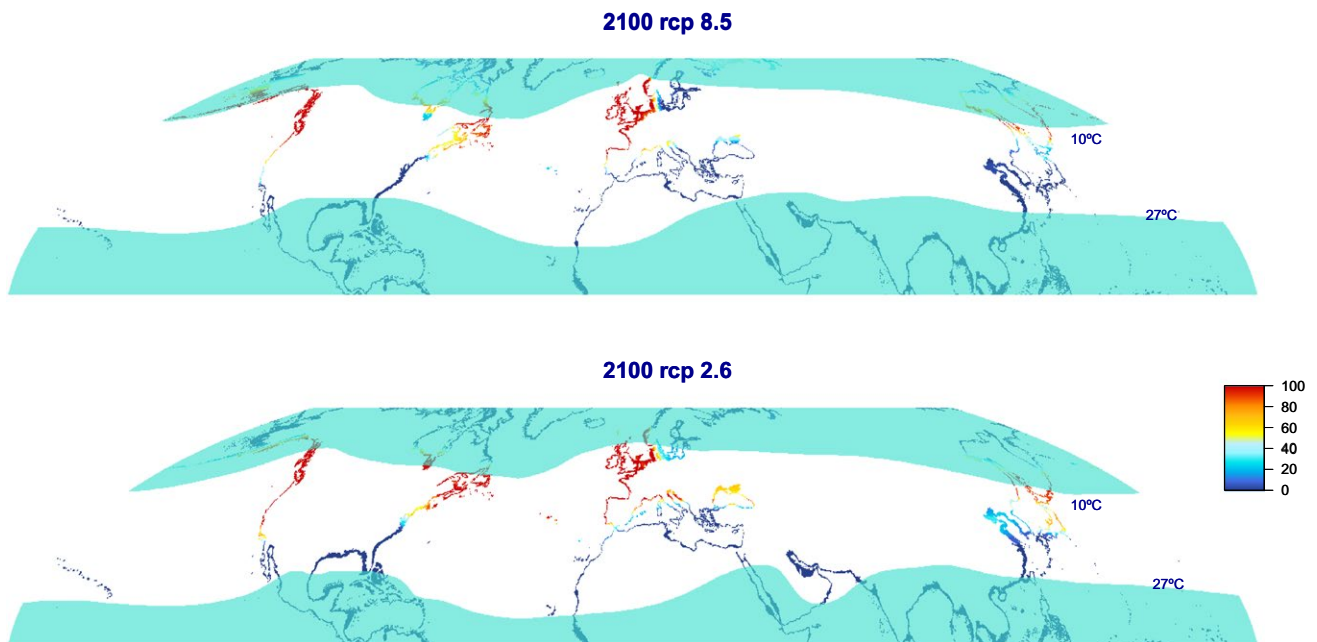


FIGURE 5 Hybrid models for *Sargassum muticum* based on the prediction by 2100 under RCP 8.5 and RCP 2.6 scenarios filtered with the mean sea surface temperature (SST) found to delimit the reproductive window at each scenario. The regions outside the limits of the SST reproductive window (isotherms of 10°C and 27°C) are in light blue colour. For instance, wide regions of North America and Asia would not be available for the reproduction of *S. muticum* under RCP 8.5, despite showing a high probability of occurrence according to the correlative species distribution model

range will be much less because of SST conditions unsuitable for its reproduction. To a lesser extent, the hybrid model also reduced the latitudinal range predicted by the correlative models under the other climatic scenarios compared. A common result for all scenarios was that, in contrast with the high probability of occurrence projected by the correlative species distribution models, large northern areas along the Pacific coasts of North America and Asia would not be available for reproduction of this species. The northernmost European coasts would not be suitable according to all except the most severe scenario. Thus, the reproductive temperature window is expected to strongly limit the northward shift of *S. muticum* distribution under future climate change.

Notable increase in distribution area of *S. muticum* was revealed under each of the four scenarios ranging from 51.48% by 2050 under RCP 2.6 (the less severe scenario) to 61.75% by 2100 under RCP 8.5. However, once filtered with the SST reproductive window, the hybrid models predicted an increase ranging from only 1.63% by 2100 (RCP 8.5) to 18.12% by 2100 (RCP 2.6). In the native range, the current distribution of *S. muticum* in China, Korea, Japan and Russia's Vladivostok Region is projected to shift northwards to Central and Northern Sakhalin, the western part of the Sea of Okhotsk, Kuril islands and Kamchatka. Despite the predicted northwards expansion in the invaded North American coasts, interestingly we also found the current habitats in Baja California and California are projected to retreat. The areas of current distribution of *S. muticum* in Southern Portugal and in Morocco (where *S. muticum* has been only very recently reported; Engelen et al., 2015) are also projected to retreat entirely. In addition, substantial risk of spread was also projected along the US East coast from New England to Newfoundland and along the Southern coast of Hudson Bay, a wide region where the species has not been introduced up to now.

The northward shift projected for *S. muticum* is in accordance with projections made for kelp forests (Assis, Araújo, & Serrão, 2018) and other furoid algae: *Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum* in the North Atlantic (Assis et al., 2014; Jueterbock et al., 2013). These studies projected that, by 2100, these temperate species will shift northwards to Arctic shores with particularly suitable habitats being found in Spitsbergen, Greenland and Canada, while currently suitable habitats below 45°N by 2200 will become unsuitable. The northward shift in *S. muticum* distribution demonstrates that this invasive seaweed species may thrive well in the future. Expansion into newly suitable habitats however requires the capacity to disperse there (Assis et al., 2017). Effective colonization of the North Atlantic and subarctic coastal habitats may be facilitated by the advantageous life history traits (e.g., reproduction by selfing, pseudo-perennial structures) and dispersal capabilities (e.g., by drifting thalli) of *S. muticum* (Engelen et al., 2015), although this may be strongly dependent on oceanographic currents (Buonomo et al., 2017). In addition, as shown by its introduction in both NE Pacific and NE Atlantic, human-mediated transport of *S. muticum* could easily facilitate its arrival and thus establishment in these newly suitable habitats. Although difficult to ascertain with high certainty, it is very likely that *S. muticum* was introduced in the past because of aquaculture trade,

in particular oyster trade (Engelen et al., 2015). Regulations are now improved regarding aquaculture transfers but the risk of accidental introductions is not null. The new areas projected here as suitable habitats could thus become colonized quite quickly through either natural or human-mediated dispersal. In its native range, *S. muticum* can be found in kelp or seagrass beds together with other *Sargassum* species and on hard substrata (Engelen et al., 2015). In addition to its ability to invade a great variety of unoccupied substrata, *S. muticum* can also invade native macroalgae assemblages and seagrass meadows if small hard substrates as pebbles, rock or oyster are available to settle on (see Engelen et al., 2015). Moreover, *S. muticum* is pseudo-perennial, with a permanent holdfast from which new axes grow annually (Arenas & Fernández, 1998; Deysner, 1984). The permanent holdfast allows individual persistence for a few years even in regions where it cannot reproduce. However, new individuals in such regions will only recruit with the arrival of migrants from suitable reproductive habitat, that is, drifting reproductive fragments that release embryos that establish there. In addition, the pseudo-perennial life cycle makes this NIS effective in dispersing because annually large pieces of thalli are released and drift with currents, and some of those possibly transport receptacles with embryos attached that may settle elsewhere. Hence, the life history traits and dispersal capabilities of *S. muticum* may endanger sensitive Arctic ecosystems, which are already in the state of shift as a result of extensive pressures from multiple anthropogenic stressors associated with the warming climate. Rising seawater temperatures are also changing indigenous seaweed species ranges (e.g., Müller, Laepple, Bartsch, & Wiencke, 2009; Assis et al., 2014), and during such range shifts they may be more vulnerable to invasions particularly, if acting in combination with changes in other environmental parameters (e.g., Brodie et al., 2014). This may lead to the redistribution of species and differentiated populations in subarctic territories with potential evolutionary consequences (Neiva et al., 2018), as well as generate cascading and irreversible impacts on local biodiversity and ecosystems.

While ecological niche models have been previously developed for various furoid seaweeds (Assis et al., 2014; Jueterbock et al., 2013; Neiva et al., 2015; Neiva, Assis, Fernandes, Pearson, & Serrão, 2014), non-indigenous seaweed species (i.e., *Halimeda*, Verbruggen et al., 2009; *Caulerpa* sp., Verbruggen et al., 2013; Chefaoui & Varela-Álvarez, 2018), and thermal physiological thresholds have been combined before with ENMs to improve seaweed predictions (Martínez, Arenas, Trilla, Viejo, & Carreño, 2015), this study is to our knowledge the first to integrate phenology data into seaweed distribution predictions. The study clearly demonstrates that including abiotic information on important phenological characteristics such as the reproductive period can affect predictions tremendously. Further studies could also assess if similar constraints are found in annual or biannual NIS (instead of semi-perennial), for which the distribution records only represent stable populations with many generations from sexual reproduction. While including SST improved the predictions of future *S. muticum* distribution, the integration of day length did not. Nevertheless, we encourage the use of our approach to incorporate day length into hybrid models for the case of species with

a narrower day length reproductive window. Fluctuations of other environmental parameters as a result of changing climate, such as salinity, concentration of nutrients or interaction with grazers could also be important to account for future ENMs (Franco et al., 2018; Kearney & Porter, 2009), although their effects might be more localized than temperatures on a biogeographical scale. In addition, incorporation of impacts from local anthropogenic stressors, such as bottom sedimentation and water turbidity, is likely to become increasingly important in a future world, even though these data are not readily available.

The reproduction-based filter had a major effect on the predicted expansion of the leading edge range, even though the number of studies that we could use were limited (5 out of 36). More data from different regions would have certainly been valuable to ascertain the variance of the reproductive window over a larger range of environments. We however do not believe that this would dramatically change our results, as the reproductive window documented so far by these studies was very large. *Sargassum muticum* is more uncommon in its native than in the invaded ranges, thus the kernel density plots show a higher number of occurrences at cooler temperatures in the invaded ranges (Figure 2). However, since the lowest SST reached by the species is similar between the native and invaded ranges (Table S3.1 in Supporting Information Appendix S3), it is likely that the species was already pre-adapted to the thermal ranges of the non-native conditions. The question of shifts in phenology and in physiology requirements following introductions is also to be further addressed (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). With the data obtained so far, which mostly rely on local studies, it is uncertain to which extent physiological requirements are stable over various regions in similar environments. In another invasive seaweed, the Pacific kelp *Undaria pinnatifida*, Murphy et al., (2016), Murphy et al., (2017) showed that using physiological data (e.g., growth or survival as a function of irradiance or SST) obtained in the native range perfectly predicted data observed in the field in the introduction range. Whether such conservatism also holds in *S. muticum* requires further studies. Similarly, ENMs rely on the assumption of niche conservatism. Benefitting from the introduction of *S. muticum* in different regions, comparative analyses of the ecosystems colonized by this seaweed would be particularly interesting to carry out to better examine putative realized niche shifts following the introduction process, as an outcome of acclimatization and adaptive evolution processes (Guisan et al., 2014; Chefaoui & Varela-Álvarez, 2018).

As *Sargassum muticum* is a phenotypically plastic species, new conditions generated by changing climate (i.e., increasing temperature and CO₂ levels, decreasing pH) may favour this species as it might be able to increase its competitive ability (Dukes, 2007). This may affect the entry pathways of these species, as well as its colonization, establishment, and future spread (Capdevila-Arguelles & Zilletti, 2008). In addition, intraspecific differences between invasive lineages of seaweeds in environmental requirements and niche dynamics have rarely been investigated (but see Chefaoui & Varela-Álvarez, 2018). Deeper understanding of the genetic and epigenetic factors that contribute to the invasive success of *S. muticum* may

further improve predictions of its future spread and identify potential impacts on native ecosystems.

Up to now, projections were only made to forecast changes of *S. muticum* in two dimensions (i.e., horizontal/latitudinal distribution and abundance). Future research would benefit from a modelling approach that would incorporate vertical depth/intertidal height shifts, as occurring in deeper habitats or lower on the shore is a documented response of seaweed to seawater temperature changes (e.g., Assis et al., 2018; Pearson, Lago-Leston, & Mota, 2009); also documented for demersal fish (Dulvy et al., 2008). Range shifts and expansion in subtidal habitats could similarly occur in subtidal seaweeds. Because the upper and lower limits of seaweed distribution may be controlled by many distinct factors (e.g., Hurd, Harrison, Bischof, & Lobban, 2014), variations in other parameters as a result of climate change may result in further distributional shifts (Harley, 2011). The first consequence of long-term increases in temperature and intertidal thermal and desiccation stress (Harley, 2003), may be that the upper limits of intertidal seaweeds will shift downwards (Harley & Paine, 2009), as shown for other fucoids (Pearson et al., 2009). This may however not be the case for seaweeds that resist thermal stress by the protective effects of desiccation, for which the upper fast-drying habitat might be the most favourable (Mota, Engelen, Serrao, & Pearson, 2015).

In conclusion, this study emphasizes the importance of considering physiological constraints on future predictions. Under the assumption of conservatism of niche and reproductive physiological constraints over space and time, we used windows of sea surface temperature (SST) suitable for reproduction along the distribution to produce more reliable forecasts. We demonstrated how the distribution of *S. muticum* may expand under different climate change scenarios and the restrictions on northward shifts by the species imposed by the SST related reproductive window. By 2050 and by 2100, under the RCP 2.6 scenario the environmental changes would result in moderate distributional shifts. In contrast, under RCP 8.5 scenario by 2100 the invasion of *S. muticum* is projected to significantly shift northwards with a partial retreat from the currently occupied southern regions. However, this northward shift is strongly reduced when the reproductive window is taken into account. Such a shift in the distribution of *S. muticum* in response to climate change may have significant ecological consequences for subarctic coastal ecosystems. As this species is highly tolerant and opportunistic, it may potentially displace native species populations in the regions where its distribution will be expanding. In addition, as it has been demonstrated to be a very good disperser, it may colonize these areas before range shifting natives do. In contrast, some habitats currently occupied by *S. muticum* (e.g., its Asian native range) will no longer be suitable and may be occupied by other seaweed species that may benefit from newly available habitats. This may result in further impacts and cascading effects on local ecosystems (Mineur et al., 2015).

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DATA ACCESSIBILITY

The occurrence and the reproductive phenology data that support the findings of this study are available within the paper [and its supplementary information files]. Dryad Digital Repository. <https://doi.org/10.5061/dryad.n090827>

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BIOSKETCHES

This study is the result of a collaborative work among researchers pertaining to the Centre for Marine Sciences (CCMAR) and the Station Biologique de Roscoff. We have a wide range of interests within marine ecology, evolutionary biology and biogeography. Much of our research is focused on forecasting marine species, notably marine forests, responses to climate change and on examining biological invasion processes in coastal areas.

Author contributions: E.A.S., A.H.E. and R.M.C. conceived the ideas; A.S. collected the data; R.M.C. analysed the data; R.M.C. and A.S. led the writing; E.A.S., A.H.E. and F.V. interpreted data and edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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