

Predicted fundamental niche expansion of *Agarophyton vermiculophyllum* under present and future climate scenarios

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Research Article

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Abstract

The introduction of new species in marine ecosystems is a phenomenon that has grown in recent years due to anthropogenic activities and climate change effects. *Agarophyton vermiculophyllum*, a red seaweed native from the north-eastern Pacific, has successfully colonised large regions in the Northern Hemisphere; however, there are no studies to date investigating how future climate conditions will affect its potential biogeographical range. In this investigation, we implemented species distribution models (SDMs) based on sea surface temperature (SST) and salinity to determine the potential current, and future distribution of *A. vermiculophyllum* based on two climate scenarios (Representative Concentration Pathways [RCP 2.6 and RCP 8.5]). The model built for *A. vermiculophyllum* showed a high discriminatory ability and marked sensitivity. The SDM for present climate settings showed a potential wider distribution than is recorded to date. In addition, a subtle habitat expansion of 2.9° into higher latitudes was reported under the RCP 2.6 scenario by the end of this century. The high carbon emission scenario (RCP 8.5) delivered a potential large habitat expansion (6.0°), even reaching arctic latitudes. Under this climate scenario, it was also observed a remarkable habitat loss of 11° in its southern distribution range. SMDs also forecasted suitable areas for this species in the Southern Hemisphere, pointing toward a potential global expansion in the coming decades. The information reported in this study is relevant to developing management plans to effectively implement contingency actions addressing invasion events, thereby fostering adequate habitat conservation policies.

1. Introduction

Climate change and the introduction and spreading of non-native species represent real threats for marine ecosystems generating changes in native biodiversity, creating novel biological interactions, and altering the provision of ecological services (Rilov and Crooks 2009). Global warming is expected to affect marine species distribution ranges creating novel habitats potentially available to be colonized by non-native species (Gorman et al. 2017). Marine traffic and aquaculture have been identified as two of the main vectors of invasion in marine systems, favouring long distance transportation of sessile organisms like seaweeds (Rilov and Crooks 2009; Hu and Juan 2013). As a result, macroalgae invasions have been recorded in most parts of the globe, although their ecological impacts remain largely unknown (i.e. Hu and Juan, 2013; Davidson et al. 2015).

The red algae *Agarophyton vermiculophyllum* (Gurgel, Norris & Fredericq), previously known as *Gracilaria vermiculophylla* (Ohmi), is native to the north-western Pacific coast of Japan, China and Korea (i.e. Terada and Yamamoto 2002; Krueger-Hadfield et al. 2017). This is a perennial and foundation species that create highly productive habitats and nursery grounds for fish and invertebrates, providing other ecological functions including CO₂ uptake and sequestration, organic carbon production and nutrient recycling (Thomsen et al. 2007; Abreu et al. 2011; Haram et al. 2020). Temperature, irradiance and salinity have been identified as the most important environmental variables controlling its physiological, growth and reproductive responses (Thomsen et al. 2007; Nyberg and Wallentinus 2009; Gorman et al. 2017). *Agarophyton vermiculophyllum* has become one of the most widespread invasive macroalgae in the

Northern Hemisphere (Kim et al. 2010; Hu and Juan, 2013). This species was firstly recorded in non-native regions over both coasts of the Atlantic Ocean, the Mediterranean Sea and the eastern Pacific coasts in the early 2000s (Bellorin et al. 2004; Rueness et al. 2005; Sfriso et al. 2010). Its introduction in new regions has been linked to oyster's culture followed by an expansion to other sites due to secondary vectors such as fouled gear, birds, boats and other vessels (Thomsen et al. 2007; Hu and Juan 2013).

In native areas, this species is usually found as gametophytes and tetrasporophytes in wave-exposed habitats attached to hard substrata such as rocks or calcareous organisms; while in non-native regions it is mainly distributed in soft sediments in sheltered estuarine and mudflats areas as unattached tetrasporophytes (Abreu et al. 2011; Krueger-Hadfield et al. 2016). This species is characterised by a great morphological plasticity, fast propagation, and the capacity to synthesise chemical defences against grazers (Nyberg and Wallentinus 2009; Gorman et al. 2017; Surget et al. 2017). These capabilities make *A. vermiculophyllum* a great competitor for resources and habitat allowing this species to colonize a wide variety of environments like coastal lagoons or intertidal habitats (Hu and Juan 2013). However, there are no reports to date assessing how future climate conditions will affect its potential habitat distribution.

In this study, we aimed at investigating the changes in the biogeographical range of *A. vermiculophyllum* expected during this century by implementing Species Distribution Models (SDMs) based on surface thermal and salinity fields. We hypothesise that this species will continue expanding its fundamental niche and will potentially colonize novel habitats as climate change progresses.

2. Methodology

2.1. *Agarophyton vermiculophyllum* occurrences and environmental variables

The data set on the distribution of *A. vermiculophyllum* was compiled from diverse sources such as published articles and databases (e.g. the Global Biodiversity Information Facility [GBIF, www.gbif.org/]) (Table S1). In addition, we added a new location from our study site in the northwest of Spain, Galicia (latitude: 42.30956, longitude: -8.62582), where this species is usually found coexisting with *Zostera marina* and *Z. noltei* in intertidal and upper subtidal areas. In this location, we are currently conducting research studies assessing the ecological impacts of *A. vermiculophyllum* in seagrass ecosystems and in shellfishing grounds.

Species distribution models (SDMs) have been widely implemented to predict the potential suitable habitat distribution of marine species, including primary producers, in response to abiotic environmental descriptors, also defined as fundamental niche (i.e. Verbruggen et al. 2013; Beca-Carretero et al. 2020). To conduct the SDMs and spatial analyses of the target species we used temperature and salinity predictors available for present conditions and future climate scenarios (years 2040-50 and 2090-2100) (Tyberghein et al. 2012, www.bio-oracle.org). These two variables have been identified among the most relevant

factors explaining growth responses and habitat distribution of marine primary producers including *A. vermiculophyllum* (Thomsen et al. 2007; Nyberg and Wallentinus 2009; Gorman et al. 2017).

We used two contrasting greenhouse gas concentration scenarios: RCP 2.6 (representative concentration pathway; low carbon emission scenario) and RCP 8.5 (high carbon emission scenario) (IPCC, 2014) (Tyberghein et al. 2012, www.bio-oracle.org). Collinearity of the environmental variables at the regional scale (presence of the species) was assessed from the Pearson correlation coefficient. Variables with a positive significant correlation with $r > 0.85$ were excluded from the spatial analyses. Specifically, mean salinity was excluded due to its high collinearity ($r > 0.85$) with minimum and maximum salinity. We run the models with a final set of five environmental descriptors: mean, maximum and minimum SST values and maximum and minimum surface salinity. The variables used in the SDMs had a 30 arc-seconds spatial resolution.

2.2. Species distribution model (SDMs)

SDMs were applied to investigate the potential variation in the fundamental niche of *A. vermiculophyllum* experienced during this century based on temperature and salinity variables. The model was built with the following assumptions: (i) the presence of *A. vermiculophyllum* in a given location, gathered from the literature review, has remained constant since its first record (Fig. 1a), (ii) the presence of the target species is in equilibrium with the current climate settings.

In this study, we implemented the MAXENT model, based on a maximum-entropy algorithm and characterised by robustly performing using only occurrence datasets (Elith et al. 2006). MAXENT generated a continuous raster file with a pixel value ranging from 0 to 1, with 0 representing the absence of the target species, and 1 representing the highest probability for potential habitat suitability. The predicted probabilities derived from the SDMs were transformed into binary maps with two categories: suitable or unsuitable habitat for the presence of the species. To assume the potential habitat suitability of *A. vermiculophyllum*, the logistic threshold “equal training sensitivity and specificity” was set as 0.156 (Table S2).

The model was calibrated using a random sample of 70% of the presence of the target species at a global scale, and later validated by selecting a random 30% of the distribution data of the species. The calibration was conducted 5 times using different random distributions of the target species. To evaluate the model, we used two different approaches. The first approach was based on “sensitivity”, which is the proportion of the presence of the species adequately forecasted by the model (Allouche et al. 2006). The second evaluation approach was based on the threshold-independent metric “Area under the curve” (AUC) and “Receiver operating characteristic (ROC)”; ROC values ranging from 0.5 to 0.7 indicated a poor prediction by the SDM; outcomes between 0.7 and 0.9 have a moderate discriminatory ability, and SDM outcomes with values higher than 0.9 were considered to predict with high robustness (Manel et al. 2001). The significance of the AUC was assessed by implementing a cross-validation procedure covering 100 interactions. Final distribution maps of the target species were obtained based on the average of the five independent predictions.

Lastly, we implemented density curve analysis to estimate shifts in latitudinal distribution (% of frequency) for habitat colonisation of the target species by 2100 based on SST and surface salinity under both climate scenarios (RCP 2.6 and 8.5) in the Northern Hemisphere (Brown et al. 1984). Density analyses were conducted using ggplot2 package with R software.

3. Results

This study includes an updated review of the distribution of *A. vermiculophyllum* at a global scale (Fig. 1a Table S1).

Based on the conducted literature review, *A. vermiculophyllum* is currently distributed in its native region (Northwest Pacific Ocean) from 21.5 to 45.3°N, covering a latitudinal distribution of ~23.8°, over a SST range of 8.6-19.6°C. In non-native regions, it is distributed over a latitudinal range from 22.6 to 58.9°N and a SST range of 7.5-26.9°C (Fig. 1a, Table 1). Particularly, this species is currently living at maximum SST of $26.9 \pm 0.1^\circ\text{C}$ and $26.6 \pm 2.2^\circ\text{C}$ in the Mediterranean Sea and the Northeast Atlantic Ocean, respectively, and minimum SST of $3.0 \pm 4.6^\circ\text{C}$ and $5.8 \pm 4.7^\circ\text{C}$ in the Northwest Pacific Ocean and the Northeast Pacific Ocean, respectively (Table 1). This species inhabits coastal waters with maximum salinities of 32.8 ± 1.2 and a minimum of 26.9 ± 3.0 .

The scores of the relative contribution of the environmental descriptors indicated that the most relevant factors explaining the distribution of *A. vermiculophyllum* were minimum salinity (40.2%) and minimum temperature (32.5%), followed by mean temperature (22.3%) and finally, with minor importance, maximum temperature (2.9%) and mean salinity (2.1%) (Table S3). The SDM built for *A. vermiculophyllum* for present climate settings based on temperature and salinity showed a potential wider distribution (12.1° to 65.1°N) than that recorded to date (21.5 to 45.3°N).

Table 1

Summary of the environmental descriptors including minimum, maximum and mean temperature (°C), and maximum and minimum salinity, of the biogeographical regions of *Agarophyton vermiculophyllum*

	Mean Temp.	Max. Temp.	Min. Temp.	Max. Salinity	Min. Salinity
Northwest Pacific Ocean	11.6 ± 2.1	19.3 ± 1.1	3.0 ± 4.6	30.4 ± 5.3	21.3 ± 10.7
Northeast Pacific Ocean	16.3 ± 3.9	25.6 ± 2.9	5.8 ± 4.7	33.0 ± 2.4	28.5 ± 4.8
Northwest Atlantic Ocean	15.0 ± 5.6	20.2 ± 5.9	10.8 ± 4.6	32.9 ± 1.6	27.3 ± 5.0
Northeast Atlantic Ocean	17.4 ± 3.5	26.6 ± 2.2	9.3 ± 5.1	33.7 ± 1.5	30.2 ± 2.8
Mediterranean Sea	17.6 ± 0.3	26.9 ± 0.1	7.4 ± 1.1	33.8 ± 1.0	27.2 ± 2.4
Average values	15.6 ± 2.2	23.7 ± 3.3	7.2 ± 2.7	32.8 ± 1.2	26.9 ± 3.0

The SDMs predicted a northward latitudinal expansion, and a habitat regression in its southern latitudinal distribution range as climate change progresses during this century, however, these trends differed in the two tested climate scenarios, RCP 2.6 and RCP 8.5. The simulation performed under the RCP 2.6 scenario predicted an average 2.0° northward expansion of the habitat suitability by 2040-2050 (Fig. 2a). However, this expansion is projected to increase to an average of 3.1° from its current predicted habitat suitability (65.1° N) under the high carbon emission scenario (RCP 8.5). By 2100, a northward expansion reaching latitudes of 68° N was inferred under the RCP 2.6 conditions, and extended to subarctic latitudes (71.1° N) under the RCP 8.5 climate scenario. Southern habitat regression patterns expected by 2100 were also more accentuated under the RCP 8.5 scenario. Thus, a 1.0° regression of its southern distribution limit is expected under the RCP 2.6 scenario, whereas 11.0° are predicted under the RCP 8.5 scenario (Fig. 1b and c, Fig. 2a). In addition, density analyses forecasted a northward latitudinal displacement of the potential maximum abundance of *A. vermiculophyllum* of ~ 2.2° under the RCP 2.6 from present conditions to 2050 and 2100 (Fig. 2b). On the contrary, it was observed a northward latitudinal displacement of the potential maximum abundance of the target species of ~2.8° and 21.1° under the RCP 8.5 from present conditions to 2050 and 2100 respectively (Fig. 2c). Lastly, the SDM built for *A. vermiculophyllum* also forecasted suitable habitats based on temperature and salinity drivers in the Southern Hemisphere in north Australia and in South American coasts at latitudes ranging from 28 to 38° S (Fig. 1bc).

4. Discussion

In this study, we evaluated how current and predicted changes in temperature and salinity over the next century could favour the habitat expansion of *Agarophyton vermiculophyllum* at a global scale. The spread and colonisation of marine macroalgae in non-native regions over the last decades is a phenomenon that has been linked to human activity and global warming, and is expected to intensify during this century as climate change progresses (Rilov and Crooks 2009; Gorman et al. 2017). Some of the most notorious and successful settlements of non-native macroalgae species have been reported in the Mediterranean Sea by *Caulerpa racemosa* or in the North Atlantic Sea by *Sargassum muticum* and *Rugulopterix okamurae* (i.e. Rilov and Crooks 2009; Davidson et al. 2015).

Agarophyton vermiculophyllum is a recent, but well-establish species in non-native regions such as in the Northeast Pacific Ocean covering a latitudinal distribution of ~23.8° (Bellorin et al. 2004; Rueness et al. 2005; Sfriso et al. 2010) (Fig. 1a). The results from the SDM built for the present scenario pointed out that this species may potentially be found in a wider latitudinal distribution in non-native regions than which is presented to date based on temperature and salinity settings (Fig. 1b). However, some factors including the absence of transport vectors, such as ships or boats, or the lack of human activities such as aquaculture, may constrain its dispersal and colonization in further areas. Besides, diverse local factors including biological interactions, or the absence of adequate substrates can limit the settlement of *A. vermiculophyllum* in novel habitats (Abreu et al. 2011; Gorman et al. 2017; Sotka et al. 2018). Lastly, other reasons counting the lack of monitoring programmes to early detect the presence of this species, or the difficulty of differentiating from other native species such as *Gracilaria asiatica* or *Gracilaria verrucosa*, may explain its underestimation in more non-native regions (Terada and Yamamoto 2002; Krueger-

Hadfield et al. 2017; Gorman et al. 2017). We suggest to perform field assessments to check the presence of the target species in those areas where our SDMs forecasted its presence but it is not recorded to date. For example, in the Southern Hemisphere, the presence of *A. vermiculophyllum* might go unnoticed due to the occurrence of other species of this genus.

The most important environmental variables explaining the distribution of *A. vermiculophyllum* were minimum salinity and minimum temperature. This is probably explained because temperatures below 3°C and salinities below 21.5‰, may represent a physiological threshold for growth and survival of this species in natural environments, hence limiting its presence in higher latitudes (i.e. Abreu et al. 2011). In this regard, previous experimental studies with non-native specimens of *A. vermiculophyllum* reported a great tolerance to survive in temperatures ranging from 5 to 34°C and salinity conditions ranging from 2 to 60‰ (i.e. Gorman et al. 2017). Mean temperatures were also relatively important explaining the spatial distribution of *A. vermiculophyllum*, probably deriving from the presence of this species in temperate regions characterized by the absence of extreme thermal ranges. Notoriously, in non-native areas, *Agarophyton vermiculophyllum* is exposed to both lower and higher SST than in its native area (Table 1). This suggests that the species has been able to increase its thermal niche in comparison with specimens from its native habitat, an observation also reported by Sotka et al. (2018), who observed higher tolerance for thermal stress in non-native species than in native species. This phenomenon was previously found in the seagrass *Halophila stipulacea*, with non-native specimens from the Mediterranean Sea being able to acclimate to colder conditions than those from native regions in the Red Sea, also suggesting a shift in its thermal niche (Beca-Carretero et al. 2020; Wesselmann et al. 2020).

Our study reports two contrasted scenarios of potential habitat expansion of the fundamental niche of *Agarophyton vermiculophyllum* based on temperature and salinity as climate change progressed during this century. Under the low carbon emission scenario (RCP 2.6), the fundamental niche remained rather stable, and habitat regression was barely found. However, under the high carbon emissions scenario (RCP 8.5), a great potential expansion of its biogeographical range was forecasted, being able to colonize large regions of the Northern Hemisphere, reaching even arctic latitudes (~71° N). In addition, the predicted increment in frequency and duration of extreme climate events such as storms and hurricanes can generate the emergence and dispersal of new fragments of marine macroalgae invasive species fostering its arrival and spread in novel habitats (Thomsen et al. 2007; Rilov and Crooks 2009). The potential successful colonization of this species in non-native regions does not always negatively impact the local communities and several ecological services are reported by the invasive *A. vermiculophyllum* (see Table 2) including shelter and refuge for juvenile stages of multiple species, the increase in the ecological complexity of coastal ecosystems, the creation of novel and positive biological interactions with native species or even its contribution to restoring ecosystem functionalities that may have been degraded as a result of the loss of native species (i.e. Surget et al. 2017; Ramus et al. 2017). In addition, *A. vermiculophyllum* is also used in a diversity of applications providing economic value, such as seaweed aquaculture in native and non-native regions such as in Japan and the Adriatic Sea in Italy to produce agar-agar or used as a biofilter for aquaculture (i.e. Abreu et al. 2011; Sfriso et al. 2020). Therefore, the results provided here point out potential regions where sustainable commercial aquaculture might be

developed as long as risk analyses were previously undertaken. Noteworthy, one of the main differences between native and non-native populations of *Agarophyton vermiculophyllum* is the low-genetic diversity found in the former one as a result of the dominance of asexual reproduction (Kim et al. 2010). This phenomenon has been previously recorded in other successful invasive macroalgae like *Caulerpa taxifolia* since this type of reproduction enables seaweeds to rapidly spread once they found new habitats (Jousson et al. 2000; Krueger-Hadfield et al. 2016). However, this characteristic could become a handicap for the long-term maintenance of new populations as low genetic diversity can compromise the resilience, and lastly the survival, of specimens against environmental disturbances, particularly those occurring within the framework of climate change (Wernberg et al. 2018; Krueger-Hadfield 2019). Moreover, the predicted loss of distribution in native areas of this engineering species can negatively affect native biodiversity, ecological functionality and trigger drastic ecosystem changes as was previously observed in marine coastal habitats (Benedetti-Cecchi et al. 2001).

Table 2

Application and effects recorded for *Agarophyton vermiculophyllum* present in non-native areas. Ecological effects are strongly linked to its ecosystem engineer performance and environmental risks are associated with high biomass episodes of this seaweed.

Level	Type	Description	References
Economical	Industry	<ul style="list-style-type: none"> • Production of agar • Soil conditioner • Potential source of nutrients • Sustainable fish packaging • Compounds with industrial and medical applications • Bio-filter for nitrogen forms in eutrophic systems or aquaculture farms 	Abreu et al. 2011; Pacheco et al. 2020; Sfriso et al. 2020; Samantha et al. 2020
Ecological	Ecosystem services	<ul style="list-style-type: none"> • Nursery habitats • Substratum for epiphytes and invertebrates • Reduce wave erosion • Enhanced of biodiversity and habitats niches • Source of detritus • Refugee from predators • Stabilization of the sediments 	Abreu et al. 2011; Gorman et al. 2017; Ramus et al. 2017; Surget et al. 2017; Keller et al. 2019; Besterman et al. 2020; Haram et al. 2020

Level	Type	Description	References
	Interactions with organisms	<ul style="list-style-type: none"> Association with the polychaete <i>Diopatra cuprea</i> Facilitation in the formation of vegetative fragments by <i>Littorina littorea</i> and <i>Diopatra cuprea</i> Competition with native seagrass and macroalgae Potential positive interaction with <i>Zostera marina</i> (based on our personal observations) 	Abreu et al. 2011; Gorman et al. 2017; Keller et al. 2019; Besterman et al. 2020
	Environmental Risks	<ul style="list-style-type: none"> Limit oxygen flow in sediment causing anoxia and sulphidic poisoning of native species Increase mortality of native organisms Sediment accumulation Reduce heterogeneity in the long term affecting specialized organism 	Gorman et al. 2017; Ramus et al. 2017; Keller et al. 2019; Besterman et al. 2020

Our results provide the first projections of the potential variation in the fundamental niche of *Agarophyton vermiculophylla* under current and future climate scenarios. They are of interest due to the ecological implications and the potential commercial interest associated with habitat colonization by this species. However, our outcomes should be interpreted with caution. Our SDMs only used available climate information for present and future climate scenarios, however, other relevant environmental descriptors such as wave action, irradiance or pH, or even factors operating at a local scale such as current velocity, nutrients, or sediment type may alter the habitat suitability predicted in this study. Yet, our species distribution maps may be useful to develop management tools to anticipate the potential colonization patterns of *A. vermiculophylla*, thus contributing to the design and implementation of contingency plans to mitigate its impact in novel habitats.

Declarations

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Figures

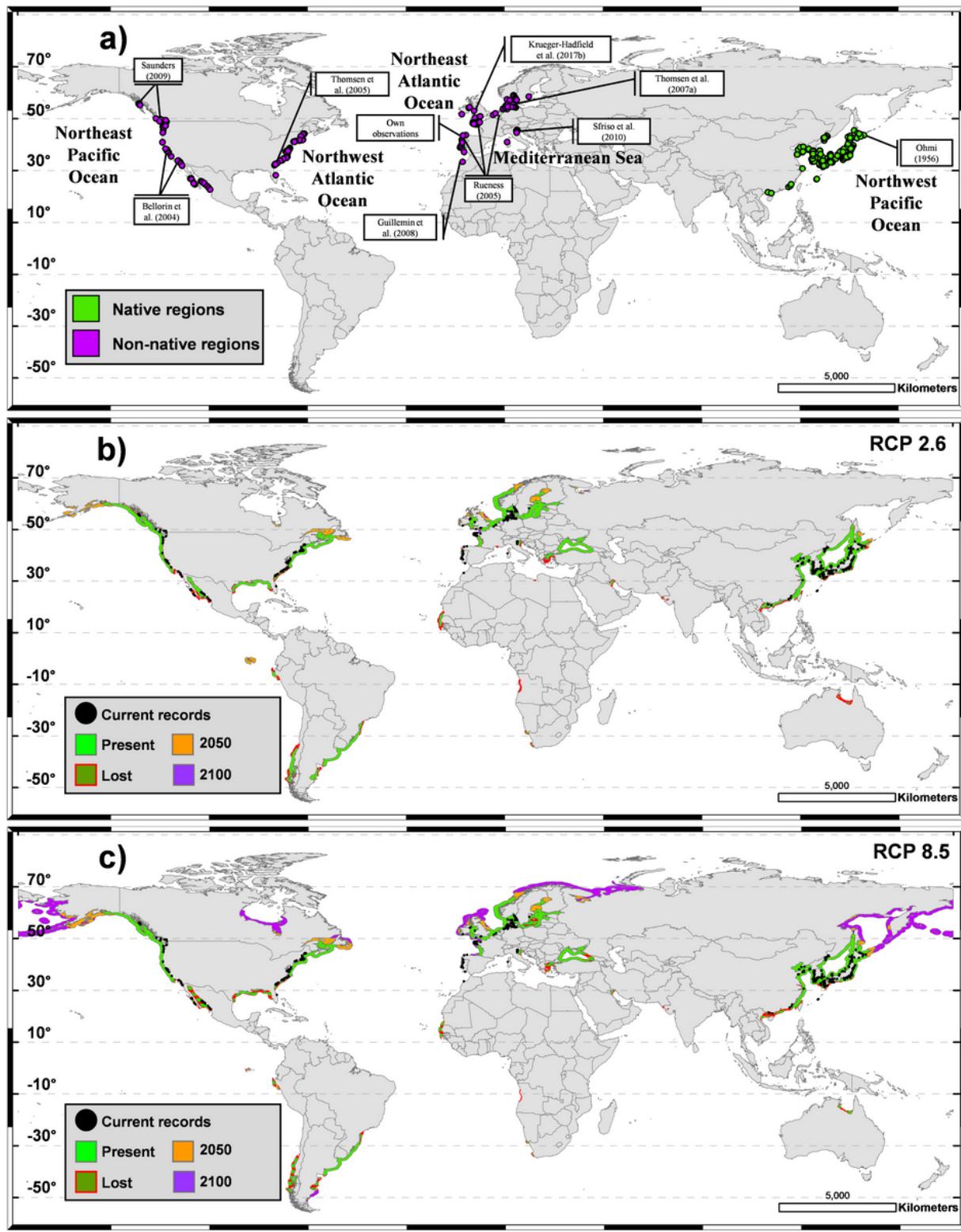


Figure 1

Map of the current distribution of *Agarophyton vermiculophyllum* showing native (green points) and non-native populations (purple points) (Panel A). References in Panel A represent the first records of *A. vermiculophyllum* in non-native regions. Maps of the potential habitat distribution based on temperature and salinity descriptors build for *A. vermiculophyllum* under present conditions of temperature and

salinity and under predicted future climate change scenarios (RCP 2.6 [Panel B] and RCP 8.5 [Panel C]) by 2050 and 2100

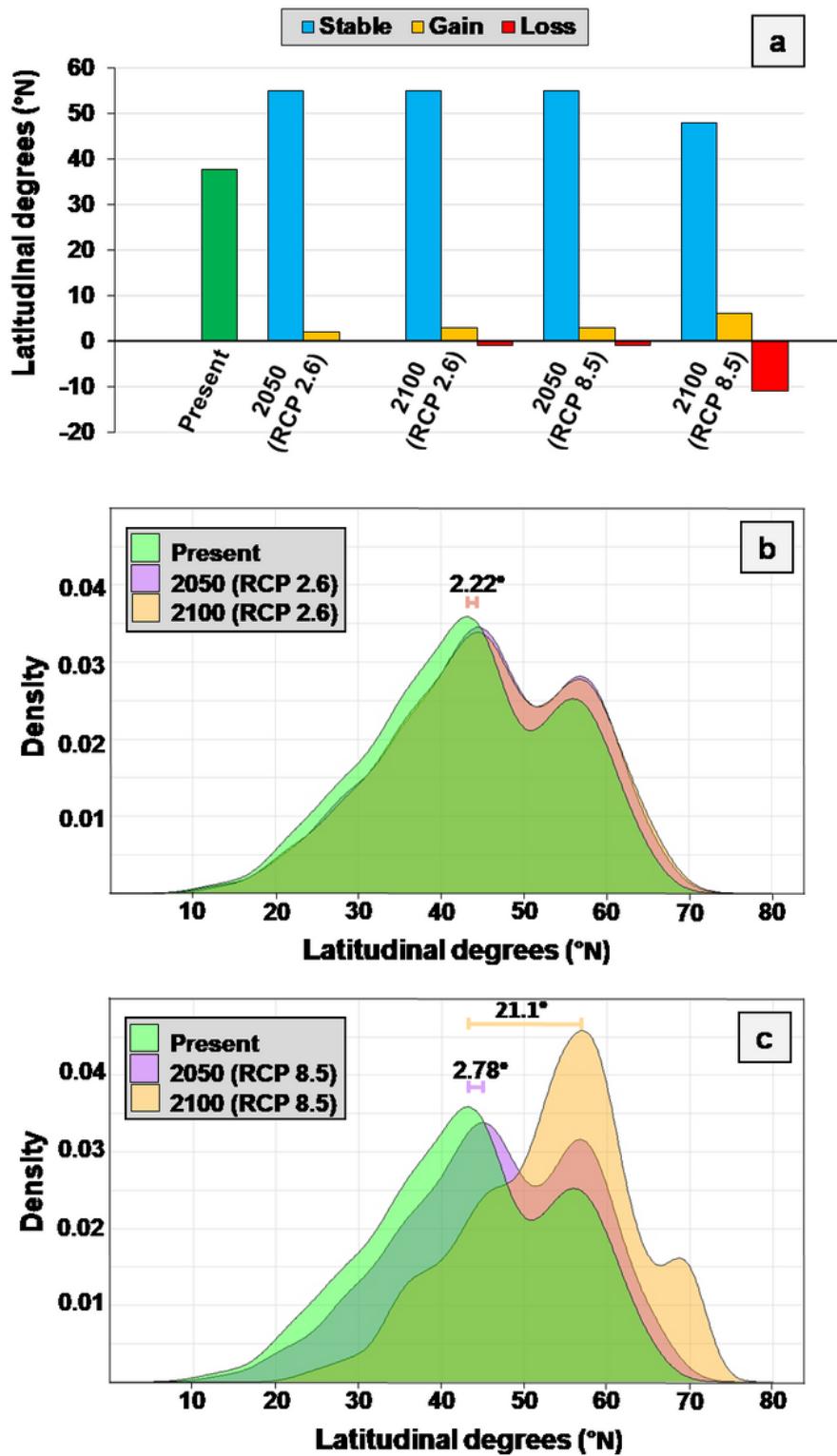


Figure 2

Current distribution (green bar), and variations in habitat suitability of *Agarophyton vermiculophyllum* in the Northern Hemisphere under present conditions and under future climate change scenarios predicted for two carbon emission scenarios (RCP 2.6 and RCP 8.5) by 2050 and 2100. Variations in distribution are expressed in latitudinal degrees (°). Blue colour represents the stable distribution, yellow represents gain distribution and red represents loss habitat distribution (Panel A). Probability density curves show more favourable latitudinal (°) regions for habitat colonization of the target species based on SST and surface salinity under both RCP (2.6 [Panel b] and 8.5 [Panel c]) climate scenarios by 2050 and 2100. Displacements in the maximum abundance distribution (% of frequency) of *A. vermiculophyllum* by 2100 are shown above each curve for both carbon emission scenarios

Supplementary Files

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