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Future distributional shift of *Eucheuma denticulatum* (Rhodophyta, Solieriaceae) under climate change in the Indo-Pacific

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Abstract

Eucheuma is one of the most important commercial red seaweeds in Southeast Asia, and plays globally an important role in seaweed aquaculture. Its natural distribution has been affected by global warming in recent years. We used maximum entropy species distribution models (SDMs) to map suitable habitat of *Eucheuma denticulatum* under present conditions and to project future range shifts under four representative concentration pathway (RCP) scenarios. The environmental factors that could best discriminate suitable from non-suitable habitat included distance to shore, water depth and sea surface temperature. Range Shifts in the distribution of *E. denticulatum* indicated that until year 2100, its range will contract in the Central Indo-Pacific Realm, especially to the Sunda Shelf, and will expand polewards along the south coast of Australia. Our results provide important knowledge for tropical seaweed conservation, management and sustainable exploration in the future.

Keywords:

Eucheuma denticulatum, global warming, maximum entropy model, range shift, suitable habitat

Introduction

Eucheumatoids, comprising the genera *Kappaphycus* and *Eucheuma*, are red seaweeds of commercial importance in tropical regions and are valuable resources for manufacturing the different types of carrageenans (Naseri et al., 2020). The countries in which Eucheumatoids are currently cultivated, including Indonesia, Philippines, Malaysia, Vietnam, etc (Borlongan et al., 2017), contribute tremendously to the world's seaweed production. Eucheumatoids grows naturally in tropical coastal environments, at temperatures ranging from 22° C to 30° C (Borlongan et al., 2017; Doty, 1973; Glenn and Doty, 1981; Kumar et al., 2020; Lideman et al., 2013), and display a rich variety of morphological plasticity (Conklin et al., 2009). According to currently known records, *E. denticulatum* is mainly distributed in the Indo-Pacific Ocean between 20° S and 30° N, between 30° E (East Africa) and 180° E (Fiji), recently extending further east to Hawaii through human activity. It grows strongly attached to coralline gravelly-rocky or coarse sandy-rocky substrate at the intertidal to the upper (shallow) subtidal zone (Carpenter and Niem, 2001). Its survival, growth, and reproduction are mainly affected by temperature, salinity, seawater current, and water depth (Hurtado et al., 2008; Zhu et al., 2014).

In recent years, many seaweeds' distributions were influenced by the increase in global warming (Smale, 2020), and are predicted to further shift poleward, extending into high latitudes and losing habitat at their trailing edges (Jueterbock et al., 2013; 2016; Muller et al., 2009; Zhang et al., 2019). The impact of global warming on tropical and subtropical seaweeds is poorly studied. As tropical seaweed, *E. denticulatum* is sensitive to rising temperatures (Somero, 2010; Tomanek, 2010), and thus, is expected to undergo range shifts in the future.

By linking occurrence data of species to the physical and biotic environment, species distribution models (SDMs) provides a framework to formulate hypotheses about the ecological processes governing spatial and temporal patterns in biodiversity, which can be useful for marine ecosystem management and conservation. In recent studies, species distribution models have become powerful management tools in wide-range climate change studies in the marine environment (de la Hoz et al., 2019). Here we focus on SDMs constructed via maximum entropy using the program Maxent (Phillips, 2017), this approach performed particularly well in a recent comparison of alternative SDMs construction methods (Elith et al. 2006). By combing the program ArcGIS (Kozak, et al., 2008), we visualized MaxEnt results and performed the spatial calculation.

With the combination of SDMs and ArcGIS, we predicted the habitat suitability for *E. denticulatum*. Based on the most important environmental factors limiting the its geographical distribution, we predicted its range shifts and migratory paths of the distribution center (centroids) for the current and future (the 2050s and 2100s). With these projections we aimed to identify which regions remain suitable for sustainable seaweed production in the tropical and subtropical Indo-Pacific regions under projected global warming.

2 Material and Methods

2.1.Study area

Based on the distribution range of *E. denticulatum* taken from occurrence data (below), we defined the studies focus area between 25°E and 180°E longitude, and between 40°S and 50°N latitude (Fig. 1). This area covered the entire Indo-Pacific Ocean, including the Western and Central Indo-Pacific Realms (Spalding et al., 2007). Background points (similar to pseudo-absence points in practice) were used to indicate the environmental conditions within the distributional range of *E. denticulatum*. The environmental conditions in the study region were compared between background points and the seaweed's occurrence sites during model evaluation. In total, 10,000 background points were randomly sampled in the study area within 100 m water depth (Barve et al., 2011; Doty, 1973; Nelson et al., 2015) (Supporting Information Fig. S1).

2.2. Species occurrence data

We assembled the occurrence records of the species *E. denticulatum* from the Global Biodiversity Information Facility (http://www.gbif.org) (GBIF.org, 2022), the AlgaeBase (https://www.algaebase.org) (AlgaeBase, 2022), the Ocean Biodiversity Information System (http:// iobis.org) (OBIS, 2022), and the AquaMaps database (https://www.aquamaps.org) (AquaMaps, 2022), and the literature (Supporting Information Table S1). We compiled a total of 172 records observed after the year 1990, and removed duplicated and on-land sites. All the online databases were accessed on March 29, 2022, and the initial filtering processing for distributed data was conducted in R 4.1.2 (R Core Team, 2017).

The records data were further filtered with the followed steps, (i) keep only one record per 5-arcmin and removed other records randomly within the same grid; (ii) only retain sites in our defined study region; (iii) perform spatial thinning using a distance of 10 km using the R package "spthin", discarding sites that were less than 10 km apart (Aiello-Lammens et al., 2015). After filtering, we finally retained 111 records for *E. denticulatum* (Varela et al., 2014; Veloz, 2009).

2.3. Environmental variables

From the Global Marine Environment Datasets (http://gmed.auckland.ac.nz; Basher et al., 2014), we obtained the 2 geographical predictors:water depth and distance to shore. From the Bio-ORACLE database version 2.2 (https://www.bio-oracle.org) (Assis et al., 2018), we obtained surface layers of 18 environmental variables (including the annual mean, the annual maximum, the annual minimum, the annual range, an average of the minimum records per year and the average of the maximum records per year) for sea surface temperature (SST), sea surface salinity (SSS) and current velocity (CV) (Supporting Information Table S2). The marine environmental predictors from Bio-ORACLE v2.2 represent the average and range values for the duration between 2000 and 2014.

Further, we used the four representative concentration pathway (RCP) scenarios (i.e., RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) and the two periods (i.e., the 2050s: the average for 2040-2050, and 2100s: the average for 2090-2100) to predict the future distribution of *E. denticulatum*. The 18 environmental variables from the Bio-ORACLE database were projected to future conditions, while the two geographical predictors (water depth and distance to shore) were assumed unchanged in the future (Zhang, et al., 2020). All environment variables are scaled to a 5-arcmin resolution. To exclude the influence of collinearity and reduce the model complexity, we calculated the correlation coefficients (r) among the environmental variables, and randomly eliminated one among highly correlated predictors ($|r| > 0.75$) (Dormann et al., 2013) (Supporting Information Fig. S2). The retained environmental variables were used for habitat suitability projections (Table 1).

2.4. Modeling method selection

Initially, we considered five modeling algorithms with their default settings in the "sdm" R package (Naimi and Araújo, 2016): generalized linear model (GLM, Guisan et al., 2002), random forest (RF, Breiman, 2001), maximum entropy (Maxent, Phillips et al., 2006), boosted regression trees (BRT), and bioclim (climate-envelope-model, Booth et al., 2014). The five models were run with the filtered occurrence data and non-correlated environmental predictors. We used for each of 10 runs a partition of 75% sub-sampled training data to fit the models, and a partition of 25% of the data to test the models' performances.

Model performance was assessed with the AUC (area under the receiver operating characteristic curve) and TSS (the true skill statistic). Because the Maxent models performed best (Supporting Information Fig. S3 and Table S3), we used this for the following analyses (Supporting Information Fig. S4-S12; Table S4-S5; Fig. 2-5; Table 1-2).

2.5. Model optimization and evaluation

2.5.1. Tuned process

The regularization multiplier (RM) and feature classes (FC) in the MaxEnt algorithm are used to balance model fitness and complexity (Phillips and Dudı´k, 2008). The applied RM and FC parameters were adjusted and optimized with filtered occurrence records and environmental data. through the R package "ENMeval" (Muscarella et al., 2014) with the assistant package "kuenm" (Cobos et al., 2019). We established a total of 240 candidate models with different combinations of regularization multipliers (ranging from 0.1 to 4.0, at a 0.1 interval) and feature classes: L (linear), LQ (linear quadratic), T (threshold), H (hinge), Q (quadratic), QH (quadratic hinge).

A spatial block method was selected for evaluating the model performance, briefly, each study region was divided into four spatial blocks containing an equal number of presence records; three blocks were used for model training and the remaining block for validation. This method takes model transferability into account (Kass et al., 2021). The best-performing model was selected with the sequential criteria, (i.e., first, minimum average 10% omission rate (OR_{10}) was used to select optimal models, followed by the highest average validation AUC ($AUC_{val.}$). All evaluation metrics were visualized in the Supporting Information Fig. S4.

2.5.2. Evaluated metrics

The performance of the Maxent models was evaluated based on 5 metrics. First, AUC, the area under the receiver operating characteristics curve, was calculated on the validation data, measuring the model's ability to discriminate between presence and background records. The values > 0.90 were considered "excellent" and in the range of 0.7–0.9 "reasonable predictions". We also used the partial ROC ratio (pROC), a modified AUC metric that is calculated through R package "kuenm" (Cobos et al., 2019). The statistic ratio >1 represents more significant than the null expectations (Peterson, 2008). What's more, the Maxent models were assessed with the Continuous Boyce index (CBI), it varies from -1 to 1, positive values indicate model predictions are consistent with the presence distribution in the evaluation dataset, values close to zero mean that the model is not different from a chance model, negative values indicate an incorrect model (Hirzel et al., 2006). In addition, we calculated $AUC_{Diff.}$ (i.e., the difference between training and testing AUC), that is positively associated with the degree of model overfitting (Muscarella et al., 2014). The two types of threshold-dependent metrics of omission rate were used for measuring model overfitting degrees: the minimum training presence' omission rate (OR_{MTP}) (Peterson et al., 2011), and the 10% training omission rate (OR_{10}) (Fielding and Bell, 1997, Peterson et al., 2011). The values greater than zero typically indicate model overfitting for OR_{MTP}, for OR_{10}, the values above 10 mean model overfitting.

2.5.3. Null models application

Null-model could indicate whether the relations between species' presence localities and the predictor variable values in the study area are stronger than can be expected by chance, and test for the significance and effect sizes of calculations metrics (Bohl et al., 2019; Raes and ter Steege., 2007). We first run the null simulations with 100 iterations to get a reasonable null distribution for comparisons with the tuned model. Null models were generated by randomly drawing collection localities without replacement from background points, which settings are the same as the tuned model (i.e. RM=2.4, FC=LQ). Then we calculated metrics (i.e. OR_{10} and $AUC_{val.}$) comparing the model performance of the the tuned and null models results. Finally, we made plots of both kinds of model evaluation results as a histogram and a violin plot (Supporting Information Fig. S5). All steps were conducted using ENMeval 2.0.0 (Kass et al., 2021).

2.6. Model construction

2.6.1. Model fitting, testing and projection

We built a Maxent model based on the 111 filtered data (Supporting Information Table S1) and eight selected environmental variables (Table 1), and projected it onto four RCP scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) for future periods (the 2050s and 2100s). Each model was based on 10 replicated runs with random sub-sampling of 75% training and 25% testing data from the set of occurrence sites. The output was set to logistic format, which yields continuous values of habitat suitability for the species, ranging from 0 to 1 (Phillips and Dudı´k, 2008).

2.6.2. The assessment of environmental variables

Relative contributions of environmental variables to the model gain (Table 1) were tested with a jackknife test (Phillips, 2017) (Supporting Information Fig. S6). We also plotted response curves showing the effect of the single environmental variables on projected habitat suitability (Supporting Information Fig. S7).

2.7. ArcGIS visualization

The model results were fed into ArcMap 10.4.1, to plot projections for two recognized representative concentration pathways (RCPs): RCP 2.6 and RCP 8.5. The plots contains continuous distribution maps (Fig. 2 and Supporting Information Fig. S8), binary distribution maps (Supporting Information Fig. S9) and distribution change maps (Fig. 3 and Supporting Information Fig. S10). The centroid shift map is in Fig. 4 for RCP 6.0 and RCP 8.5.

The continuous habitat suitability projections were loaded into ArcMap 10.4.1 (Fig. 2), to calculate average probabilities of suitability to allow calculating threshold values (0.43) discriminating suitable from non-suitable habitats (Liu et al., 2005). Based on this threshold, we converted the continuous habitat suitability for *E. denticulatum* to binary values (0 or 1) (Supporting Information Fig. S9). These maps were transformed to the Equal-Area Cylindrical projection to calculate distribution changes (Table 2 and Fig. 3), and the distribution centers (centroids) (Fig. 4). From these distribution centers, we could estimate migration paths under climate change (Supporting Information Table S4).

2.8. Extrapolation, Clamping and Multivariate Environmental Similarity Surfaces (MESS)

The multivariate environmental similarity surfaces (MESS) analysis measured the differences in the environmental conditions between present-day occurrence records and study regions in the present and future using the R package “rmaxent” (Baumgartner and Wilson, 2021; Elith et al., 2010), which could reflect the degree of extrapolations risk (Supporting Information Fig. S11). When environmental conditions at a pixel fall well out of the range of values the model was trained with, the extrapolation will become unreliable, ‘clamp’ assumption should be applied in this case, meaning they will be set to the maximum value captured by training samples. The values shown in the clamp pictures give the absolute difference in predictions when using vs not using clamping (Supporting Information Fig. S12). Predictions were interpreted only with an assessment of clamping predictions.

3 Results

3.1. **Model optimization and evaluation**

The best one (tuned model) of the 240 candidate models was characterized by RM=2.4 and feature class=LQ. By the null simulation, the $AUC_{val.}$ and OR_{10} exhibited significant differences between the tuned and null models (Supporting Information Fig. S5), indicating both metrics were valid to the models applied, and the tuned model performance was much better than that of null models (Supporting Information Fig. S5).

Among 240 candidate models, the tuned model exhibited the lowest OR_{10} (0.0600±0.0741) and highest $AUC_{val.}$ (0.8204±0.0215), suggesting that the model was not overfitted, and could well discriminate test records from background localities (Hanley and McNeil, 1982), respectively. Low $AUC_{Diff.}$ values also supported the model's low risk to overfit (0.0313±0.0218). Besides, the large pROC value (2.044±0.029) indicated that the model was superior to the null expectations with statistical significance. The CBI_{test} value (0.6947±0.2762), suggested that the predicted model matched well with the *E. denticulatum* occurrence records (Supporting Information Fig. S4; Table S5).

3.2 Clamping and MESS

The MESS value in the areas north of 40°N and south of 30°S was below -50, which means that this region showed large differences in environmental conditions compared with the conditions in the present occurrence records, indicating a high risk of extrapolation. The MESS values were slightly negative in the Sunda Shelf, which implies that there was a slight risk of extrapolation to environmental conditions that the species does not experience in its present range of distribution (Supporting Information Fig. S11). The MESS maps for future predictions were highly similar to the MESS map for present-day conditions, but showed overall slightly larger negative values, suggesting that the future environments in the region will exceed values experienced in the present range of distribution. MOD (most different environmental variables) maps show the variables that were the most different from variables at the occurrence locations. In the future, these were SST_{range} and SST_{mean}, especially in Central Indo-Pacific Realm.

The values shown in the clamp pictures give the absolute difference in predictions when using vs not using clamping (Supporting Information Fig. S12). The values were lower for the present day and future map, indicating the predicted area is less affected by variables being outside their training range.

3.3. The assessment of environmental variables

3.3.1. Variable contributions analysis

After eliminating the environmental variables with a correlation of $|r|>0.75$ (Supporting Information Fig. S2), we retained 8 environmental variables (Table 1): distance to shore (land distance), water depth, annual range of sea surface temperature (SST_{range}), annual mean of sea surface temperature (SST_{mean}), annual range of sea surface salinity (SSS_{range}), annual mean of sea surface salinity (SSS_{mean}), annual mean of currents velocity (Cv_{mean}), and annual min of currents velocity (CV_{min}). According to the permutation importance to the model, the distance to shore contributed the highest (57.4%), SST_{range} ranked second (11.2%), and SST_{mean} ranked fourth. CV_{mean} and CV_{min} ranked third and fifth, respectively. The accumulated permutation importance of the three most important environmental factors reached 76%.

3.3.2. Jackknife test

The Jackknife test results showed that the distance to shore and water depth were the most effective variables of the model (Supporting Information Fig. S6 a), and SST_{range} was also was also an important factor in *E. denticulatum* distributions (Supporting Information Fig. S6 b). All the data are from the 10 replicate runs (Supporting Information Fig. S6).

3.3.3. Response curves of environmental variables

Habitat suitability decreased with increasing SSS_{range}, but increased with increasing SSS_{mean}, CV_{min}, and CV_{mean}. Concerning the SST_{range} and SST_{mean}, the habitat suitability showed an optimum at ca. 7°C and 23°C, respectively, and a drop towards smaller and higher values (Supporting Information Fig. S7). When setting the threshold for suitable habitat to 0.43, the suitable ranges of key environmental variables were: SST_{mean} between 20°C and 29°C, SST_{range} between 2.5°C and 12.5°C, SSS_{range} between 0 and 4.0 PPS, and SSS_{mean} between 32.5 and 40 PPS. The distance within 500 km was negatively correlated with the habitat suitability, therefore 0-50 km shore distance was considered suitable to the seaweed distributions.

3.4. Prediction of potential distributions

3.4.1. Continuous and binary distributions

In the Central Indo-Pacific Realm, *E. denticulatum* was predicted to find suitable habitats in Malaysia, Indonesia, the Philippines, Vietnam, and Australia (Fig. 2). In the Western Indo-Pacific Realm, it was predicted to find suitable conditions in the Arabian Province, Red Sea and the Gulf of Aden Province, and also at places scattered along the east African coast. In coastal areas above

30° in latitude, the species was predicted to be sparsely distributed.

Presently, *E. denticulatum* occupied 18.3% of the suitable habitat in the near-shore regions. Under the 2050 RCP 2.6 scenario, its niche occupation decreased to 16.7%, then decreased further to 16.6% under the 2100 RCP 2.6 scenario. In the RCP 8.5 scenario, niche occupation was 16.2% and 14.1% for the 2050s and 2100s respectively (Table 2). Generally, the difference in predicted suitable habitats between the four scenarios was significant. With the increasing severity of representative Concentration pathways (RCPs), the proportion of suitable habitats decreased gradually (Fig. 5), suggesting that the distribution of *E. denticulatum* is affected by gas emission and global warming.

3.4.2. Distribution changes

We predict that the suitable habitat of *E. denticulatum* will shrink in the Central Indo-Pacific Realm, especially on the Sunda Shelf, including most regions of Malaysia and Indonesia; while its distribution will remain comparatively stable from Djibouti to South Africa; central Australia will be also less variable; the range along the Arabian coasts will contract slightly. The models predict *E. denticulatum* to extend its range e along the south coast of Australia (Fig. 3). In general, the range contraction will be much larger than the range expansion, especially in the Central Indo-Pacific Realm, and this might be our further focus area to conduct seaweed resource research in the future.

E. denticulatum's northern distribution boundary was predicted to contract less than its southern boundary. With increasing severity of the representative concentration pathways (RCPs), the species' poleward range expansion was predicted to decrease and the lower latitude range was predicted to increasingly contract except for the case of RCP 6.0 (Fig. 3).

Compared with the conditions in occurrence data, the most different variable in the future was sea surface temperature (SST_{mean} and SST_{range}) (Supporting Information Fig. S11), particularly in regions where its future distribution was predicted to change significantly (i.e. the Central Indo-Pacific Realm).

3.4.3. Centroid changes

The centroids and their changes under the four RCP scenarios were predicted to move about 170-425 km south-westward from south of Indonesian waters (coordinates: 100.187, -2.34158) in equatorial regions (Fig. 4); the migration distance would increase with the increasing severity of the representative concentration pathway (except under the RCP 4.5 scenario) (Supporting Information Table S4).

4. Discussion

Present-day distribution projections and environmental drivers

Based on the MaxEnt model, distance to shore, water depth and sea surface temperature are identified as the most important variables delimiting the distribution of *E. denticulatum*. The response curves indicated that *E. denticulatum* finds suitable habitat where SST_{mean} remains above 20 °C and currents velocity is relatively high, which is consistent with physiological and biochemical studies (Borlongan et al., 2017; Kumar et al., 2020; Lideman et al., 2013) and literature record (Carpenter and Niem, 2001). The suitable habitat range of *E. denticulatum* is centered within 30°S and 30°N in the Central and Western Indo-Pacific Realm, which matches the currently available distribution information of *E. denticulatum*. However, our prediction of the coverage of the currently suitable distribution area in this region is only 18.3%, which is much lower than simulations on AquaMap website (Kaschner eet al., 2019) and our expected results.

First, the less available distribution data due to incorrect species identification may cause an underestimate of the potential distribution of *E. denticulatum*. The morphological plasticity of Eucheumatoids may cause *E. denticulatum* to be misidentified as *Kappaphycus* species, especially in the early stage, when relying only on morphological observation and farmer experience to identify species (Conklin et al., 2009). On the other hand, Lim et al (2014) have found the unexpected low *Eucheuma* species coverage compared with *Kappaphycus*, and the biodiversity of *Eucheuma* species was scarce according to molecular analysis throughout Southeast Asia. Thus the actual natural distribution of *E. denticulatum* in the Indo-Pacific Realm may not be promising, and this situation will be exacerbated by future global warming. The genetic and distribution situation for *E. denticulatum* remains to be studied by broadly sampling expeditions in the future.

Range shifts and its consequences under climate change

Seawater temperature is expected to increase with global warming (Muller et al., 2009). In our study, many regions were predicted to become unsuitable for *E. denticulatum* distribution under the future RCP scenarios, especially in the Sunda Shelf in the Central Indo-Pacific Realm, which should be of special interest to conservation planners. Besides, we predict range expansion along with the south coast of Australia and range contraction in equatorial regions under the predicted southward movement. These findings provide the first step to understanding the climate change response of tropical red seaweeds, to predict changes in Eucheumatoids production in the future.

As a raw material for the extract of carrageenan, Eucheumatoids are widely cultivated in Southeast Asia countries, mainly Indonesia and the Philippines owing to the suitability of climate and environmental conditions (Lim et al., 2014). It reached production of 10,831,200 tons in the world in 2018 (including 1,597,300 tons of *Kappaphycus alvarezii* and 9,237,500 tons of *Eucheuma spp.*) (here *Eucheuma spp.* mainly refers to *E. denticulatum*) (FAO. 2020), serving as a source of livelihood to tens of thousands fisherfolks in Southeast Asia. However, in our study, the suitable habitat would decrease most significantly under the four future climate scenarios in the Sunda Shelf, which includes most regions of Malaysia and Indonesia. This is certainly bad news for the entire Eucheumatoids farming industry in Southeast Asia. Besides, we predicted the trend of poleward movement for *E. denticulatum*.

Accordingly, the breeding industry of *Eucheuma* needs to make appropriate adjustments. For example, future seaweed farms may need to migrate to higher latitudes to ensure suitable conditions for *E. denticulatum* growth and reproduction. In the future, the germplasm of *E. denticulatum* can be improved through artificial mutagenesis or hybridization, and the high-temperature resistant strains can be selected and cultivated for breeding and production of *E. denticulatum*, to cope with global climate change.

Prediction on optimistic distribution in the future

Our prediction results showed that most of the coastal areas of Australia were potential distribution areas for *E. denticulatum*, which was suitable for the growth of *E. denticulatum*, but there were few reports on Eucheumatoids breeding in Australian waters. The potential use-value of this area needs to be further studied. The future will still need more Marine environmental factors (pH, Chlorophyll, nutrient, etc.) and biological interactions factors (such as competition for light with microbes and grazed by sea urchins, sea stars and rabbit fish) (Mateo et al., 2021) built into the model, to evaluate the region of *E. denticulatum* comfortable by nature. Our work would provide the reference for further rational development and utilization of sea area resources.

5. Conclusion

Our study shows that *E. denticulatum* is mainly distributed in the Central and Western Indo-Pacific Realm with Indonesia as the center, which matches the current available distribution information of *E. denticulatum*. The most important environmental factors for the distribution of *E. denticulatum* include distance to shore, water depth and sea surface temperature. Based on four representative concentration pathways (RCP) scenarios, the predicted future distribution and range change indicate that by 2100, the distribution of RCP will change significantly in the central Indo-Pacific Realm especially in the Sunda shelf, while poleward along the south coast of Australia. And the southward shift of its distribution center also shows this similar trend. Our results indicate that we should be alert to the effects of future climate change on tropical algae, and make appropriate adjustments to Eucheumatoids culture and breeding industry. This study provides an important theoretical basis for the conservation of *E. denticulatum* germplasm resources, the development and utilization of new sea areas, the direction of breeding and the sustainable development of carrageenan industry. In the future, regional data should be combined to simulate regions with significant changes in range, and genetic data should be integrated to clarify the effects of future climate change on species genetic diversity and population structure, and physiological and biochemical experiments should be carried out to understand the adaptation mechanism of Eucheumatoids to climate change.

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Figure legends

Figure 1. Study region and occurrence records.

Blue triangles indicate occurrence records of *E. denticulatum* used to develop Species Distribution Models (111 points used).

Figure 2. Continuous distribution maps of *E. denticulatum* for present-day.

Continuous values from 0 to 1.0 indicate a gradual increase in habitat suitability, from blue to red in color. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

Figure 3. Distribution change maps.

Predicted range shifts of the *E. denticulatum* along Indo-Pacific coasts from present-day to 2100s under RCP 2.6 and 8.5 scenarios. Stable areas (in blue) indicate habitats that are predicted to remain suitable, contraction areas (in red) are predicted no longer to be suitable in the future; expansion areas (in purple) represent habitats that would be suitable in future. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2100S: 2090-2100.

Figure 4. The centroids change of *E. denticulatum* for RCP 6.0 and RCP 8.5 scenarios from present to 2100s.

The red sphere represents the centroid of the RCP 8.5 scenario (2050s and 2100s), while the blue sphere represents the centroid of the RCP 6.0 scenario (2050s and 2100s), the purple sphere is the centroid in the present-day. The corresponding colored line represents the centroid change route of the respective scenario. The dashed line represent the equator.

RCP: representative concentration pathway. 2050s: 2040–2050, 2100s: 2090-2100.

Figure 5. Suitable range change (%) over time.

The x-axis represents different RCP scenarios, and the y-axis represents the suitable habitat proportion. Lightblue, mistyrose and lavender color represent 2100s, 2050s, present stage , respectively.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Table legends

Table 1. Permutation importance (%) and detailed information of marine predictors in maxent model.

Values in bold indicate important predictors.

Table 2. Range size change (%) from present-day to the future under climate change.

RCP: representative concentration pathway. 2050s: 2040–2050, 2100s: 2090-2100.

Supporting material legends

Figure S1. Background points.

Background points that provided information on environmental conditions within the distributional range of *E. denticulatum* (10000 points used). We limited the study extent to water depths above 100 m (Nelson et al., 2015).

Figure S2. Heatmap of the correlation between environment variables.

The heatmap shows color-correlation between any pair of the 20 environmental variables, plotted with the R package ‘corrplot’. The darker the color, the stronger the correlation. We eliminate one among highly correlated predictors (|r| > 0.75) (Dormann et al., 2013).

SSS: sea surface salinity, CV: Current velocity , SST: sea surface temperature, Land_distance: distance to shore.

Figure S3. The Maxent ROC for five models.

The receiver operating characteristic curve (ROC) for five models method for 10 runs. The deep red line represents the average training AUC (area under the receiver operating characteristic curve) of ten runs; the deep blue line represents the average test AUC of ten runs. The value > 0.90 were considered “excellent” and in the range 0.7–0.9 “reasonable predictions”.

rf: random forest; maxent: maximum entropy; brt: boosted regression trees; glm: generalized linear model.

Figure S4. Evaluation results of Maxent model performance.

The auc.val and or.mtp values as performance indicators for models (average over 10 replicate models) with different feature classes (fc). The color of the points and lines represents the regularization multiplier (rm). auc: validation of area under the receiver operating characteristic curve. Values > 0.90 were considered “excellent” and in the range 0.7–0.9 “reasonable predictions”. or.mtp: the minimum training presence’omission rate. Values >0 typically indicate model overfitting.

Figure S5. Comparison between null models and tuned model performance.

(a) Histogram and (b) violin plot of evaluated metrics. auc: validation of area under the receiver operating characteristic curve. Values > 0.90 were considered “excellent” and in the range 0.7–0.9 “reasonable predictions”. or.10: 10% training omission rate. This value than the expectation of exceeds 10% typically indicates model overfitting (Fielding and Bell, 1997; Peterson et al., 2011)

Figure S6. The results of the jackknife test.

The results of the jackknife test showing (a) variable importance using training gain, (b) variable importance using test gain, and (c) AUC on test data. Values shown are averages over 10 replicate runs. AUC: validation of area under the receiver operating characteristic curve. bio2 and 6 are annual mean and range of sea surface temperature; bio8 and 12 are annual mean and range of sea surface salinity; bio14 and 15 are annual mean and min of currents velocity; bio89: water depth;

bio90: distance to shore.

Figure S7a-h. Response curves of the eight environmental variables.

The curves show how the mean (red line) logistic probability of the presence of *E. denticulatum* depends on each variable over10 replicate models; the range of two standard deviations is represented as a blue shade.

SSS: sea surface salinity, CV: Current velocity , SST: sea surface temperature, Land_distance: distance to shore.

Figure S8a. Continuous distribution maps of *E. denticulatum* for the future (the 2050s and 2100s) conditions under different climate change scenarios (RCP 2.6 and RCP 8.5).

Continuous values from 0 to 1.0 (blue to red) indicate a gradual increase in habitat suitability. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Figure S8b. Continuous distribution maps of *E. denticulatum* for the future (the 2050s and 2100s) conditions under different climate change scenarios (RCP 4.5 and RCP 6.0).

Continuous values from 0 to 1.0 (blue to red) indicate a gradual increase in habitat suitability. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Figure S9a. Binary distribution maps of *E. denticulatum* for present-day and future (the 2050s and 2100s) under different climate scenarios (RCP 2.6 and RCP 8.5).

The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Figure S9b. Binary distribution maps of *E. denticulatum* for future (the 2050s and 2100s) under different climate scenarios (RCP 4.5 and RCP 6.0).

The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Figure S10a. Distribution change maps.

Predicted range shifts of *E. denticulatum* along Indo-Pacific coasts from present-day to 2050s under different climate scenarios (RCP 2.6, 4.5, 6.0, 8.5). Areas predicted to remain suitable (in blue), to become unsuitable (in red) , and to become suitable (in purple) in the future. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050.

Figure S10b. Distribution change maps.

Predicted range shifts of the *E. denticulatum* along Indo-Pacific coasts from the 2050s to 2100s under different climate scenarios (RCP 2.6, 4.5, 6.0, 8.5). Stable areas (in blue) indicate habitats that are predicted to be suitable, contraction areas (in red) are predicted no longer to be suitable; expansion areas (in purple) represent habitats that would be suitable in the future. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2050s: 2040–2050, 2100s: 2090-2100.

Figure S10c. Distribution change maps.

Predicted range shifts of the *E. denticulatum* along Indo-Pacific coasts from present-day to 2100s under different climate scenarios (RCP 4.5 and RCP 6.0). Stable areas (in blue) indicate habitats that are predicted to be suitable, contraction areas (in red) are predicted no longer to be suitable in the future; expansion areas (in purple) represent habitats that would be suitable in the future. The solid lines represent the equator and the dashed lines represent the tropic of capricorn and tropic of cancer.

RCP: representative concentration pathway. 2100S: 2090-2100.

Figure S11. Multivariate environmental similarity surface (MESS) maps and most different environmental variables (MOD) maps.

Lower negative values indicate increasingly different climatic conditions between present-day and future scenarios, and higher positive values increasingly similar conditions (Elith et al., 2010). The MOD map shows which variable was most different compared with conditions in occurrence data.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Figure S12. The clamp maps.

These pictures showed where the prediction is most affected by variables being outside their training range. The values shown in these pictures give the absolute difference in predictions when using vs not using clamping (Clamping means that environmental variables and features are restricted to the range of values encountered during training). Warmer colors show areas where the treatment of variable values outside their training ranges is likely to have a large effect on predicted suitability.

RCP: representative concentration pathway. 2050s: 2040–2050. 2100s: 2090-2100.

Table S1. Ocurrence records and source of *E. denticulatum.*

Table S2. Twenty marine environmental variables

They were considered to be relevant for habitat suitability of *E. denticulatum*.

Table S3. Comparison of model performance between different modeling methods.

AUC: area under the receiver operating characteristic curve; TSS: the true skill statistic. For AUC, models with values > 0.90 were considered “excellent” and in the range 0.7–0.9 “reasonable predictions”. For TSS, models with values > 0.8 were considered “excellent” and in the range 0.4–0.8 “good”.

RF: random forest; Maxent: maximum entropy; BRT: boosted regression trees; GLM: generalized linear model.

Table S4. The coordinates and shifts of *E. denticulatum* distribution centers from today to the future (the 2050s and 2100s) under RCP 6.0 and RCP 8.5 scenarios.

RCP: representative concentration pathway. 2050s: 2040–2050, 2100s: 2090-2100.

Table S5. Eight metrics for measuring model-performance (models with different feature class and regularization multiplier).

FC: feature class. RM: regularization multiplier. AUCval.: validation area under the receiver operating characteristic curve. AUCtrain: train area under the receiver operating characteristic curve. AUCdiff.: the difference between training and testing AUC. OR10: 10% training omission rate. ORmtp: the minimum training presence’ omission rate. CBIval.: the validation Continuous Boyce index. pROC: partial Receiver Operator Characteristic ratio.

Reference

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., Anderson, R. P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541-545. https://doi.org/10.1111/ecog.01132

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrao, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modeling. Global Ecology and Biogeography 27, 277-284. https://doi.org/10.1111/geb.12693.

AlgaeBase, 2022. AlgaeBase website at. https://www.algaebase.org. (Accessed 13 March 2022).

AquaMaps, 2022. AquaMaps website at. https://www.aquamaps.org. (Accessed 13 March 2022).

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modeling 222, 1810-1819. https://doi.org/10.1016/j.ecolmodel.

Basher, Z., Bowden, D. A., Costello, M. J., 2014. Global marine environment dataset (GMED). Version 1.0 (Rev.01.2014). Available from. http://gmed.auckland.ac.nz.

Baumgartner, J., Wilson, P., 2021. rmaxent: Tools for working with Maxent in R. R package version 0.8.5.9000. https://github.com/johnbaums/rmaxent

Bohl, C. L., Kass, J. M., Anderson, R. P., 2019. A new null model approach to quantify performance and significance for ecological niche models of species distributions. Journal of Biogeography 46, 1101-1111. https://doi.org/10.1111/jbi.13573

Booth, T. H., Nix, H. A., Busby, J. R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modeling package, its early applications and relevance to most current MAXENT studies. Diversity and Distributions 20, 1-9. https://doi.org/10.1111/ddi.12144

Borlongan, I. A., Gerung, G. S., Kawaguchi, S., Nishihara, G. N., Terada, R., 2017. Thermal and PAR effects on the photosynthesis of *Eucheuma denticulatum* and *Kappaphycus striatus* (so-called Sacol strain) cultivated in shallow bottom of Bali, Indonesia. Journal of Applied Phycology 29, 395-404. https://doi.org/10.1007/s10811-016-0956-7

Breiman, L., 2001. Random Forests. Machine Learning 45, 5-32. https://doi.org/10.1023/A:1010933404324

Carpenter, K. E.; Niem, V. H. (eds), 2001. The Living Marine Resources of the Western Central Pacific, Vol. 1. FAO, Rome.

Cobos, M. E., Peterson, A. T., Barve, N., Osorio-Olvera, L., 2019. Kuenm: an R package for detailed development of ecological niche models using Maxent. Peer J 7, e6281. https://doi.org/10.7717/peerj.6281

Conklin, K.Y., Kurihara, A., Sherwood, A.R., 2009. A molecular method for identification of the morphologically plastic invasive algal genera *Eucheuma* and *Kappaphycus* (Rhodophyta, Gigartinales) in Hawaii. Journal of Applied Phycology 21, 691-699. https://doi.org/10.1007/s10811-009-9404-2

de la Hoz, C. F., Ramos, E. R., Puente, A., Juanes, J. A., 2019. Climate change induced range shifts in seaweeds distributions in Europe. Marine Environmental Research 148, 1-11. https://doi.org/10.1016/j.marenvres.2019.04.012.

Doty, M.S., 1973. Farming the red seaweed, *Eucheuma* for carrageenans. Micronesia 9, 59-71.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27-46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M. and E. Zimmermann, N., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129-151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., Kearney, M., Phillips, S., 2010. The art of modeling range-shifting species. Methods in Ecology and Evolution 1, 330-342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

FAO. 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action. Rome. https://doi.org/10.4060/ca9229en

Fielding, A., Bell, J., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24(1), 38-49. https://doi.org/10.1017/S0376892997000088

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J. A., Olsen, J. L., Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal.

Ecology and evolution 3(5), 1356-1373. https://doi.org/10.1002/ece3.541

Jueterbock, A., Smolina, I., Coyer, J.A., Hoarau, G., 2016. The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. Ecology and Evolution 6, 1712-1724. https://doi.org/10.1002/ece3.2001

Hanley, J. A., McNeil, B. J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology, 143(1), 29-36. https://doi.org/10.1148/radiology.143.1.7063747

Hirzel, A. H., Lay, G. L., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modeling 199(2), 142-152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Hurtado, A. Q., Critchley, A. T., Trespoey, A., Bleicher-Lhonneur, G., 2008. Growth and carrageenan quality of *Kappaphycus striatus* grown at different stocking densities, duration of culture and depth. Journal of Applied Phycology 20, 551-555. https://doi.org/10.1007/s10811-008-9339-z

GBIF.org, 2019. GBIF occurrence download. Accessed from R via dismo. www.gbif.org. https://cran.r-project.org/web/packages/dismo) on 2021-03-11.

Glenn, E. P., Doty, M. S., 1981. Photosynthesis and respiration of the tropical red seaweeds, *Eucheuma striatum* (Tambalang and Elkhorn varieties) and *E. denticulatum*. Aquatic Botany 10, 353-364. https://doi.org/10.1016/0304-3770(81)90033-4

Glenn, E. P., Doty, M. S., 1992. Water motion affects the growth rates of *Kappaphycus alvarezii* and related seaweeds. Aquaculture 108, 233-246. https://doi.org/10.1016/0044-8486(92)90109-X

Guisan, A., Edwards Jr, T. C., Hastie, T ., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89-100. https://doi.org/10.1016/S0304-3800(02)00204-1

Kaschner, K., Kesner-Reyes, K., Garilao, C., Segschneider, J., Rius-Barile, J. Rees, T., and Froese, R., 2019. AquaMaps: Predicted range maps for aquatic species. Retrieved from https://www.aquamaps.org.

Kass, J. M., Muscarella, R., Galante, P. J., Bohl, C. L., Pinilla-Buitrago, G. E., Boria, R. A., Soley-Guardia, M., Anderson, R. P., 2021. ENMeval2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution 12, 1602-1608.

Kozak, K. H., Graham, C. H., Wiens, J. J., 2008. Integrating GIS-based environmental data into evolutionary biology. Trends in Ecology and Evolution 23, 141-148. https://doi.org/10.1016/j.tree.2008.02.001

Kumar, Y. N., Poong, S. W., Gachon, C., Brodie, J., Sade, A., Lim, P. E., 2020. Impact of elevated temperature on the physiological and biochemical responses of *Kappaphycus alvarezii* (Rhodophyta). PLoS One 15(9), e0239097. https://doi.org/10.1371/journal.pone.0239097

Lideman, Nishihara, G. N., Noro, T., Terada, R., 2013. Effect of temperature and light on the photosynthesis as measured by chlorophyll fluorescence of cultured *Eucheuma denticulatum* and *Kappaphycus* sp. (Sumba strain) from Indonesia. Journal of Applied Phycology 25, 399-406. https://doi.org/10.1007/s10811-012-9874-5

Lim, P. E., Tan, J., Phang, S. M., Nikmatullah, A., Hong, D. D., Sunarpi, H., Hurtado, A. Q., 2014. Genetic diversity of *Kappaphycus* Doty and *Eucheuma* J. Agardh (Solieriaceae, Rhodophyta) in Southeast Asia. Journal of Applied Phycology 26, 1253-1272. https://doi.org/10.1007/s10811-013-0197-y

Liu, C., Berry, P. M., Dawson, T. P., Pearson, R. G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385-393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Mateo, J. P., Faisan, J. P., Sibonga, R. C., Suyo, J. G. B., Luhan, M. R. J., Ferriols, V. M. E. N., Hurtado, A. Q., 2021. Farm Management and Biosecurity Measures of Eucheumatoids: Cultivars, Pest and Diseases, Risks and Risk Managements. University of the Philippines, Visayas, Miagao, Iloilo, Philippines

Muller, R., Laepple, T., Bartsch, I., Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. Botanica Marina 52, 617-638. https://doi.org/10.1515/BOT.2009.080

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., Anderson, R. P., 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5, 1198-1205. https://doi.org/10.1111/2041-210X.12261

Naimi, B. and Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modeling. Ecography 39, 368-375. https://doi.org/10.1111/ecog.01881

Naseri, A., Jacobsen, C., Sejberg, J., Pedersen, T. E., Larsen, J., Hansen, K. M., Holdt, S. L., 2020. Multi-extraction and quality of protein and carrageenan from commercial Spinosum (*Eucheuma denticulatum*). Foods (Basel, Switzerland) 9(8), 1072. https://doi.org/10.3390/foods9081072

Nelson, W., Neill, K., D'Archino, R., Anderson, T., Beaumont, J., Dalen, J., 2015. Beyond diving depths: deepwater macroalgae in the New Zealand region. Marine Biodiversity 45, 797-818 https://doi.org/10.1007/s12526-014-0293-5

OBIS, 2019. Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. Accessed from R via robis. www.iobis.org. https://cran.r-project.org/web/packages/robis) on 2022-03-13.

Peterson, A. T., Papeş, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modeling 213(1), 63-72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson, A. T., Soberon, J., Pearson, R. G., Anderson, R. P., Martınez-Meyer, E., Nakamura, Nakamura, M., Araújo, M. B., 2011. Ecological Niches and Geographic Distributions. Monographs in Population Biology 49. Princeton University Press, Princeton, New Jersey, USA.

Phillips, S.J., Anderson, R. P., Schapire, R. E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190, 231-259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161-75. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips, S. J., 2017. A Brief Tutorial on Maxent. https://biodiversityinformatics.amnh.org/open_source/maxent/

Radosavljevic, A., Anderson, R. P., 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41, 629-643. https://doi.org/10.1111/jbi.12227

Raes, N. and ter Steege, H., 2007. A null-model for significance testing of presence-only species distribution models. Ecography 30, 727-736. https://doi.org/10.1111/j.2007.0906-7590.05041.x

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Smale, D.A., 2020. Impacts of ocean warming on kelp forest ecosystems. New Phytologist 225, 1447-1454. https://doi.org/10.1111/nph.16107

Somero, G. N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. Journal of Experimental Biology 213, 912-920. https://doi.org/10.1242/jeb.037473

Spalding, M. D., Fox, H. E., Fox, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57(7), 573-583. https://doi.org/10.1641/B570707

Tomanek, L., 2010. Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. The Journal of experimental biology 213(6), 971-979. https://doi.org/10.1242/jeb.038034

Varela, S., Anderson, R. P., García-Valdés, R., Fernández-González, F., 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37(11), 1084-1091. https://www.jstor.org/stable/ecography.37.11.1084

Veloz, S. D., 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography 36, 2290-2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Zhang, J., Yao, J., Hu, Z. M., Jueterbock, A., Yotsukura, N., Krupnova, T. N., Nagasato, C., Duan, D., 2019. Phylogeographic diversification and postglacial range dynamics shed light on the conservation of the kelp *Saccharina japonica*. Evolutionary Applications 12, 791-803. https://doi.org/10.1111/eva.12756

Zhang, Z., Capinha, C., Karger, D. N., Turon, X., MacIsaac, H. J., Zhan, A., 2020. Impacts of climate change on geographical distributions of invasive ascidians. Marine Environmental Research 159. https://doi.org/10.1016/j.marenvres.2020.104993

Zhu, J., Fang, Z., Liu, M., Liang, L., Huang, H., Zou, X., Lin, X., Bao, S., 2014. Effects of temperature, salinity and light intensity on the growth, pigment and carrageenan of *Betaphycus* *gelatinum*. Biocontrol Science and Technology 145(1), 135-144.

https://doi.org/10.1127/1864-1318/2014/0171