Habitat suitability and potential range shifts under projected climate change in two temperate octocorals using species distribution modelling (#64520)

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Habitat suitability and potential range shifts under projected climate change in two temperate octocorals using species distribution modelling

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Understanding how animals and plants are distributed in space and how projected changes in climate and the environment may affect the future distribution of a species are key questions in ecology. Species distribution models (SDMs) have a become a valuable tool to investigate such questions and are widely used in both terrestrial and marine species. In this study, SDMs were constructed for two shallow-water temperate octocoral species, the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*), to investigate and compare habitat preferences and suitability across the study area, defined from the Bay of Biscay to the British Isles and southern Norway. The SDMs showed that bathymetry, slope and minimum sea bottom temperatures were key drivers of present-day distribution in both species. In addition, wave orbital velocity and the proportion of rock cover were identified as important predictors of present-day distribution in *E. verrucosa* but not in *A. digitatum*, which suggests *E. verrucosa* prefers habitats with more rock cover and adequate movements of ocean currents. The SDM built for *E. verrucosa* was re-run with projected minimum bottom temperatures in 2050 and 2100 under the Representative Concentration Pathway 4.5 scenario to test whether its northern range limit (south-west England and Wales and north-west Ireland) might expand in the future. This analysis showed that some areas, for example in the eastern English Channel beyond Swanage and in the Irish Sea beyond Pembrokeshire, that are currently uninhabited may become more suitable over the next century if bottom temperatures in the study area increase. Importantly, the results from this study highlight areas of very high habitat suitability which, combined with knowledge on population density, could inform targeted conservation efforts to protect and ensure the long-term survival of priority areas.

Habitat suitability and potential range shifts under projected climate change in two temperate octocorals using species distribution modelling

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Abstract

Understanding how animals and plants are distributed in space and how projected changes in climate and the environment may affect the future distribution of a species are key questions in ecology. Species distribution models (SDMs) have a become a valuable tool to investigate such questions and are widely used in both terrestrial and marine species. In this study, SDMs were constructed for two shallow-water temperate octocoral species, the pink sea fan (*Eunicella verrucosa*) and dead man’s fingers (*Alcyonium digitatum*), to investigate and compare habitat preferences and suitability across the study area, defined from the Bay of Biscay to the British Isles and southern Norway. The SDMs showed that bathymetry, slope and minimum sea bottom temperatures were key drivers of present-day distribution in both species. In addition, wave orbital velocity and the proportion of rock cover were identified as important predictors of present-day distribution in *E. verrucosa* but not in *A. digitatum*, which suggests *E. verrucosa* prefers habitats with more rock cover and adequate movements of ocean currents. The SDM built for *E. verrucosa* was re-run with projected minimum bottom temperatures in 2050 and 2100 under the Representative Concentration Pathway 4.5 scenario to test whether its northern range limit (south-west England and Wales and north-west Ireland) might expand in the future. This analysis showed that some areas, for example in the eastern English Channel beyond Swanage and in the Irish Sea beyond Pembrokeshire, that are currently uninhabited may become more suitable over the next century if bottom temperatures in the study area increase. Importantly, the results from this study highlight areas of very high habitat suitability which, combined with knowledge on population density, could inform targeted conservation efforts to protect and ensure the long-term survival of priority areas.

Introduction

Species distribution models (SDMs), also known as ecological (or environmental) niche models (ENMs), are a class of predictive models that seek to explain how animals and plants are distributed in space and time (Guisan & Thuiller 2005). These models estimate the relative suitability of habitat in a geographical area for a particular species by using locations where a species is known to occur (presences), and in some models not occur (absences or pseudo-absences), and a suite of predictor variables that represent the terrain and environmental conditions of the study area (Elith & Leathwick 2009). SDMs have become a frequently used tool to address questions such as: what are the main ecological drivers that determine the range of a species?; what are the levels of habitat suitability in areas currently outside the known range of a species?; and how will projected changes in climate and the environment affect the future habitat suitability of a species? (Warren & Seifert 2011). From a conservation management perspective, the ability of SDMs to provide insights on these questions has led to SDMs being considered in biodiversity assessments; some of these include: identifying priority areas for restoration and/or protection; detecting and/or monitoring pathways for invasive species; and forecasting the effects of climate change on biodiversity (Araújo et al. 2019). SDMs can, however, be sensitive to the input data and to the methodology and parameters used to build the models, which means it is important to assess the accuracy and reliability of model predictions, particularly if they are to be applied in a conservation management setting (Sofaer et al. 2019). In recent times, a number of studies have been published to address these concerns which provide a set of guidelines for assembling robust SDMs to address various study objectives (Araújo et al. 2019; Feng et al. 2019; Sillero & Barbosa 2020).

SDMs have been used to investigate global habitat suitability of cold-water octocorals (Yesson et al. 2012) and regional habitat suitability in one or a few temperate and deep-water species (Tong et al. 2013; Lauria et al. 2017; Burgos et al. 2020; Georgian et al. 2020; Morato et al. 2020). These studies have revealed novel findings about which terrain and environmental factors are the most important for determining habitat suitability in the octocoral species studied and how future suitability might be affected by projected changes in climate and the environment. Such a study, however, has yet to be applied to the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*), two temperate octocoral species that are found in the north-east Atlantic. These two species are both sessile, need substrate on which to attach to, require moderate-strong water movement, and are typically recorded in coastal shallow-waters 1-50m depth (Budd 2008; Readman & Hiscock 2017). *Eunicella verrucosa* is a colonial gorgonian and is found from the western Mediterranean and north-east Africa (southern range) to south-west England and Wales and north-west Ireland (northern range). The species is considered 'vulnerable' by the IUCN Red List, and it is listed as a species of principal importance in England and Wales under the NERC Act 2006, which is reflective of its national rarity and its ecological importance as a valuable habitat provider for other benthic species, particularly when colonies form gorgonian 'forests' (Pikesley et al. 2016; Ponti et al. 2018; Chimienti 2020). *Alcyonium digitatum*, on the other hand, is a colonial soft coral and is found from Portugal (southern range) to parts of Norway and Iceland (northern range). In comparison to *E. verrucosa*, whose northern range is limited to Donegal Bay–Aghros Point in north-west Ireland, Pembrokeshire in south-west Wales and off-Swanage in southern England, *A. digitatum* is ubiquitous along all British and Irish coasts (Fig. 1). This presents an interesting opportunity to explore the ecological drivers that limit the distribution of *E. verrucosa*, but not *A. digitatum*, across Britain and Ireland.

The first aim in this study, therefore, was to explore which terrain and environmental variables are the most important predictors of present-distribution in *E. verrucosa* across its northern range and in *A. digitatum* across its middle-northern range. The second aim was to assess habitat suitability across this spatial extent in both species and potentially identify areas of suitable habitat that are currently not known to be inhabited. The final aim was to test whether habitat north of the northern range limit of *E. verrucosa* will become more suitable in 2050 and 2100 based on projected changes in sea bottom temperatures.

Materials and methods

Study area

The study area covered all seas in north-west Europe from the Bay of Biscay to the British Isles and southern Norway (Fig. 1). This area captures the northern range of the present-day distribution of *E. verrucosa* and the middle-northern range of the present-day distribution of *A. digitatum* in the north-east Atlantic Ocean.

Figure 1: Present-day distribution of the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*) across the study area. This area represents the northern range of *E. verrucosa* and the middle-northern range of *A. digitatum* in the north-east Atlantic Ocean. Presence records were extracted from the Global Biodiversity Information Facility data (GBIF) portal on 4th August 2021 (presence data were not available for the Faroe Islands on the GBIF portal but anecdotal evidence supports the presence of *A. digitatum* in the coastal waters of these islands). Image credits: Jamie R. Stevens.

Presence records

Presence-only records for both species were obtained from the Global Biodiversity Information Facility (GBIF) data portal (accessed on 4th August 2021). The gbif() function from the package dismo v1.3-3 (Hijmans et al. 2020) was used in R v4.1.0 (R Core Team 2021) to extract records for each species within a predefined geographic extent (longitude: -16.0, 9.0, latitude: 44.5, 62.75). Records were removed if they had missing data for longitude, latitude or institution code, or identifications prior to 1990. Remaining records were used to visualise the present-day distribution of both species (Fig. 1). To mitigate potential effects of survey bias among the presence records, only one point per raster cell was retained. For *E. verrucosa* this reduced the number of points from 2,778 to 318, while for *A. digitatum* this reduced the number of points from 15,807 to 1,940. Some of the raster predictor variables contained missing data at some points which reduced the final number of presence points to 273 for *E. verrucosa* and 1,527 for *A. digitatum*.

Predictor variables

A set of terrain and environmental variables were used as candidate predictors of present-day distribution (Table 1; Fig. S1). These variables were chosen based on their potential links to the habitat requirements of octocoral species (Munro & Munro 2003; Yesson et al. 2012; Holland et al. 2017). Bathymetry (depth) and slope data were downloaded from MARSPEC through Bio-ORACLE (Assis et al. 2018) using the R package sdmpredictors v0.2.9 (Bosch 2020). Minimum sea bottom temperature, minimum sea surface temperature, calcite concentration and pH were also downloaded from Bio-ORACLE using sdmpredictors. All raster data sets accessed through Bio-ORACLE had a resolution of 0.083 to 0.083 degrees and present-day data sets represent long-term averages between 2000 and 2014 (Assis et al. 2018). Rock cover, orbital velocity and tidal velocity were extracted from a data set assembled and published by the University of Strathclyde (Wilson et al. 2018). This data set covers (and is limited to) the north-west European continental shelf from the Bay of Biscay to the North Sea and the Faroe Islands at a resolution of 0.125 by 0.125 degrees (Fig. S1). Due to the difference in resolution, these rasters were resampled to match the resolution of the Bio-ORACLE rasters using the resample() function from the R package raster v3.4-13 (Hijans 2021) using the bilinear interpolation method. Collinearity between all predictor variables was evaluated using correlation tests and the variance inflation factor. The vifcor() function from the R package usdm (Naimi et al. 2014) was run using all observations in each raster variable. One variable was removed if VIF values >10 or the correlation was >0.70. Sea surface temperature was very strongly correlated with sea bottom temperature ($r = 0.97$), therefore only the latter was retained. We anticipate that bottom temperature is more likely to be ecologically relevant for the adult phase of sessile octocoral species, although sea surface temperature has been shown to affect the pelagic larval duration of a number of marine species (reviewed by Cowen & Sponaugle 2009).

Climate projection layers were sourced from Bio-ORACLE for Representative Concentration Pathway (RCP) climate scenarios 4.5 and 8.5 for the years 2050 and 2100 (Assis et al. 2018). These layers were produced by averaging data from distinct atmosphere-ocean general circulation models provided by the Coupled Model Intercomparison Project Phase 5 (Assis et al. 2018). RCP 4.5 represents a peak and decline (intermediate) scenario in greenhouse gas concentration levels ending in stabilisation, while RCP 8.5 represents a (worst-case) scenario of increasing emission over time leading to high greenhouse concentration levels. Projection layers were only available for sea temperatures, so future distributions in 2050 and 2100 were modelled based on projected values for minimum sea bottom temperature.

Background locations

Reliable absence data that detail accurately where a species is not found were not available for either octocoral species. Therefore, SDMs were constructed using presence-only data and 'background' locations in the study area. These types of models attempt to quantify statistical relationships between predictor variables at locations where a species has been observed versus randomly selected points within the study area where a species has not been found (pseudo-absence points). For *E. verrucosa*, random selection of background points was constrained to the northern limit of its present-day distribution; this ensured that background points were not sampled from beyond the potential area where *E. verrucosa* are known to occur or potentially disperse to (Fig. S2). This was performed using the randomPoints() function from dismo using the rock cover raster as a mask. Initially, 6,000 points were randomly sampled which was reduced to a final number of 5,767 background points after filtering for missing data at some predictor variables. For *A. digitatum*, the same approach was applied except that the entire study area was used for randomly selecting background points (Fig. S2). Here, 6,000 points were reduced to a final number of 5,985 background points after filtering for missing data.

Maximum entropy modelling

Maximum entropy (Maxent), a machine learning algorithm, was used to build SDMs (Philips et al. 2006; Philips et al. 2017). Maxent models were fitted to the data using the ENMevaluate() function from the R package ENMeval v2.0.1 (Muscarella et al. 2014; Kass et al. 2021). This function builds SDMs iteratively across a range of user-defined tuning settings, enabling different models to be compared and the optimal model to be selected. The Maxent algorithm from dismo (maxent.jar v3.4.4) was used to construct the models. To assess model performance, the location data were divided up into training and test sets using cross-validation, and metrics were calculated for each model. The ‘block’ spatial partition method was used for the division, which splits the presence points into four spatial groups of equal numbers (or as close as possible) that correspond to lines of latitude. The assignment of points into groups based on spatial rules attempts to mitigate spatial autocorrelation, which can overinflate model performance (Veloz 2009, Wenger & Olden 2012, Roberts et al. 2017), between points that are included in the training and validation sets. The Maxent algorithm allows the user to implement different types of models by specifying different combinations of feature classes and regularisation multipliers (Elith et al. 2011; Merow et al. 2013). The feature class determines the shape of the response curves, while the regularisation multiplier determines the penalty associated with adding more parameters to the model. For example, a linear feature class will likely result in a simpler model than a model that allows both linear, quadradic and hinge feature classes. Higher regularisation multipliers, on the other hand, impose a stronger penalty on model complexity and therefore result in smoother response curves and simpler models.

In this study, a combination of feature classes (linear, quadratic and hinge) and regularisation multipliers (1-5) were implemented using Maxent. The area under the receiver operating characteristic curve (AUC) was calculated for each model and averaged across the test sets of a particular combination (AUC_{TEST}) to assess the performance of each model to predict the species distribution. Values close to 1 indicate excellent predictive performance, while values of 0.5 indicate that the model is no better than random. To select the model with the optimal fit to the data, both AICc and a sequential method that uses the cross-validation results were examined. The sequential method selects the model with the lowest average test omission rate and then the highest AUC_{TEST} if two or more models have the same omission rate. If these two methods disagreed over the optimal model, but the predictive power (AUC_{TEST}) was very similar, the predictions of each model were inspected to inform selection of the optimal model. In addition, a null model was run and compared to the optimal model to test whether this (empirical) model differs from that of a null model. The null model was configured with the ENMnulls() function from ENMeval using the same withheld presence data and method of spatial partition as the optimal model, which enabled direct comparisons between the performance metrics of the null and the optimal model (Bohl et al. 2019; Kass et al. 2020).

Once the optimal model was selected, the percent contribution and the permutation importance of each predictor variable was extracted from the results. The percent contribution is a measure of which variables are contributing to fitting the model during training of the Maxent model (Philips 2006). The permutation importance, on the other hand, is a measure of the final Maxent model in which values of a variable are randomly permuted among the training presence and background points and the resulting value of the training AUC is recorded; a large decrease in the training AUC suggests that the model is highly dependent on that particular variable (Philips 2006). The predictions showing the probability of presence, interpreted here as areas of habitat suitability, were then extracted and visualised using functions from the R packages ENMeval and tmap v3.3-2 (Tennekes 2018). To predict future areas of habitat suitability based on projected minimum sea bottom temperatures, the present-day raster was substituted for each future raster layer and the optimal model was re-run. Future predictions of habitat suitability were then extracted for 2050 and 2100 and visualised using tmap.

Results

Model evaluation

The optimal model was selected based on the lowest AICc because the predictions for both species made more biological sense using the models derived from this metric compared to the sequential method. For *E. verrucosa*, the hinge feature class with a regularisation multiplier of 4 was identified as the optimal model, with very high predictive power ($\mathrm{AUC}_{\mathrm{TEST}} = 0.965$). For *A. digitatum*, the hinge feature class with a regularisation of multiplier of 1 was identified as the optimal model, also with very high predictive power ($\mathrm{AUC}_{\mathrm{TEST}} = 0.934$). The average difference between the value for the AUC training set ($\mathrm{AUC}_{\mathrm{TRAIN}}$) and the value for the $\mathrm{AUC}_{\mathrm{TEST}}$ was close to zero for *E. verrucosa* ($\mathrm{AUC}_{\mathrm{DIFF}} = 0.005$) and *A. digitatum* ($\mathrm{AUC}_{\mathrm{DIFF}} = 0.022$), indicating little evidence of overfitting in these models. In addition, comparison tests in both species showed that the $\mathrm{AUC}_{\mathrm{TEST}}$ of the optimal model was statistically different from a null model (*E. verrucosa*, $p = 0.001$; *A. digitatum*, $p < 0.001$).

Contribution of predictor variables

The contribution of each predictor variable to the SDMs was assessed by visualising the percent contribution and the permutation importance (Fig. 2). Among the predictors, bathymetry showed high percent contribution and permutation importance for *E. verrucosa* (25.3% and 44.1%, respectively) and *A. digitatum* (54.4% and 64.4%, respectively). For *E. verrucosa*, orbital velocity made the second highest contribution to fitting the model followed by sea bottom temperature, slope, rock cover, pH and calcite concentration. For *A. digitatum*, sea bottom temperature and slope were the only other predictors that noticeably contributed to fitting the model. In both species, tidal velocity contributed very little to predicting distribution.

Figure 2: Contribution of each predictor variable to fitting the optimal model. Proportions for percent contribution and permutation importance are shown for the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*).

Present-day predictions of habitat suitability

The probability of presence maps, interpreted here as a proxy for habitat suitability, mostly captured the distribution where both octocoral species are known to occur (Fig. 3 – see Supplementary Information for an interactive version of Figure 3). For *E. verrucosa*, for example, there are areas of high habitat suitability across north-west France and the Channel Islands, south-west England and Wales, and south-west and western Ireland. However, the SDM also predicted suitable habitat in the eastern England Channel, in northern Donegal in Ireland and in parts of western Scotland and the Outer Hebrides, all of which are not thought to harbour populations of *E. verrucosa*. For *A. digitatum*, areas of high habitat suitability were predicted across north-west and northern France, the Channel Islands, most of the British Isles, including the Shetland Islands and some offshore areas in the southern North Sea, and parts of southern Norway. The SDM also predicted suitable habitat in the Faroe Islands, despite no presence points from this location being used in training the model. In addition, compared to the present-day distribution of *A. digitatum* (Fig. 1), there was little support for habitat suitability in the central Celtic Sea. There was also a similar pattern with other coastal sites in the Netherlands, Germany, Denmark and Norway. When all probabilities are visualised, there is very low or zero probability of habitat suitability at these locations (Fig. S3).

Figure 3: Present-day maps of habitat suitability for the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*) based on Maxent species distribution models. Probability of presence is interpreted as a proxy for habitat suitability; only probabilities greater than 0.5 are shown (see Fig. S3 for maps with all probabilities).

Future predictions of habitat suitability

Future predictions of habitat suitability for RCP 4.5 (intermediate scenario) based on projected sea bottom temperatures showed some different patterns to the present-day predictions for *E. verrucosa* (Fig. 4 – see Supplementary Information for an interactive version of Figure 4). In particular, there were two key differences from present-day to future scenarios. Firstly, the model predicted that a few areas in the southern Irish Sea become more suitable in 2050, the number of which increases from 2050 to 2100; these areas are located along the coasts of western Wales and north-east Ireland. Secondly, there is an increase in habitat suitability on both sides of the eastern English Channel, the number of which also increases from 2050 to 2100. No areas in the North Sea become suitable under this intermediate scenario; however, under RCP 8.5, the model predicted suitable habitat in parts of the North Sea (Fig. S4).

Figure 4: Future predictions of habitat suitability for the pink sea fan (*Eunicella verrucosa*) based on a Maxent species distribution model. Future layers of sea bottom temperature were substituted for the present-day layer while all other layers used to originally train the model were kept; the model was then re-run to generate future predictions. Predictions for Representative Concentration Pathway (RCP) 4.5 are shown for 2050 and 2100. Probability of presence is interpreted as a proxy for habitat suitability; only probabilities greater than 0.5 are shown.

Discussion

Habitat preferences

Bathymetry and slope explained a large component of the present-day species distribution of both *E. verrucosa* and *A. digitatum* (Fig. 2). This finding is not surprisingly since topography can influence a number of processes central to octocoral survival, including sedimentation, ocean currents and food availability (Yesson et al. 2012). Interestingly, wave orbital velocity and, though to a lesser extent, rock cover were notable predictors for *E. verrucosa* but not for *A. digitatum*. This suggests that the ecological requirements of *E. verrucosa* may be more dependent on the availability of rock substrate and adequate current flow than *A. digitatum*. Indeed, *E. verrucosa* typically attaches to stable rock or other hard substrates via a basal holdfast and grows upwards and outwards towards the current flow, and, while *A. digitatum* is also found attached on such substrates, it is also capable of settling on other substratum including shells, cobble and other (unstable) coarse substrates (Wood 2013).

Tidal velocity, in comparison to orbital velocity, only had a negligible contribution to explaining the distribution of *E. verrucosa* and *A. digitatum*. This may be reflective of the fact that most colonies / populations of these two octocoral species are found in sublittoral zones and not in air-exposed intertidal zones and therefore strong tidal regimes are not generally much of an influence. Alternatively, it may indicate that wave orbital velocity is more important for bringing in fresh nutrients and oxygen, both for polyps to feed on and for exporting waste products, than tidal velocity.

Calcite concentration and pH also did not contribute as highly to explaining species distribution compared to the other variables, particularly for *A. digitatum*. This is in contrast to a global study of habitat suitability for cold-water octocorals where calcite saturation state was identified as an important factor for determining habitat suitability (Yesson et al. 2012). Availability of calcium carbonate is critical for the formation of skeletal structures in octocoral species (Conci et al. 2021), so the results in the present study suggest that the observed variation in calcite concentration and pH across the study area (Fig. 1) may be within acceptable limits for the survival of both *E. verrucosa* and *A. digitatum*. Nevertheless, ocean acidification, a reduction in pH of the ocean caused by the uptake of carbon dioxide from the atmosphere (Hoegh-Guldberg et al. 2007), is often linked with negative effects on biomineralisation and calcification, for example, in species of scleractinian corals (Mollica et al. 2018), coralline algae (Martin and Hall-Spencer 2017) and molluscs (Gazeau et al. 2013). An acceleration in ocean acidification, therefore, could alter the current acceptable limits of calcite concentration and pH across the study area and reduce the suitability of habitat in certain locations. However, octocoral species subjected to different pHs appear to show varied responses in calcification rates and sclerite structure (Conci et al. 2021), which suggests that some species may have greater resilience to ocean acidification than others.

Lastly, sea bottom temperature was identified as an important predictor for both *E. verrucosa* and *A. digitatum*. To our knowledge, as yet there are no published studies which explore the thermal minima or maxima for either of these species. Therefore, the only evidence we currently have that gives us insights on the thermal tolerances of either species are the sea temperatures at the locations where they are known to occur. Accordingly, we anticipate that the northern range of *E. verrucosa* is constrained, at least in part, by temperature and, based on seasonal marine thermoclines (Brown et al. 2003), minimum winter temperatures appear to be closely aligned with the current northern and north-eastern edges of the distribution of *E. verrucosa* in Britain and Ireland. We also envisage a similar scenario for the northern range of *A. digitatum*, though the current study is less well placed to address this because the extent of some the raster predictor variables do not cover the northern limits of the *A. digitatum* distribution. The results for *E. verrucosa* in this study appear to support this suggestion because predictions in future habitat suitability changed as projected minimum bottom temperatures changed (Fig. 4). If minimum bottom temperatures do indeed play a significant role in the survival of both species, this suggests that approximately 6.66^{o}C and 0.97^{o}C (Table 1) are the currently known thermal minima estimates for *E. verrucosa* and *A. digitatum*, respectively. However, *A. digitatum* has also been recorded in several locations north of the study area, in parts of north-west Norway and Iceland, so this species could potentially tolerate even lower temperatures.

Present-day habitat suitability

Maxent models built for both *E. verrucosa* and *A. digitatum* had very high predictive power ($AUC_{TEST} = 0.965$ and $AUC_{TEST} = 0.934$, respectively), which suggests the models perform well at capturing areas of habitat suitability (Fig. 2). For *E. verrucosa*, the optimal model indicated potentially suitable habitat in three areas beyond its northern range limit that are currently not thought to harbour populations of this species: (i) several inshore and offshore areas west and east of the Isle of Wight in the eastern English Channel; (ii) northern Donegal in Ireland; and (iii) parts of western Scotland and the Outer Hebrides. However, the probability of habitat suitability across these areas was generally less than 0.6, with only a few isolated areas showing high suitability (probabilities greater than 0.8). There are three likely explanations for the discrepancy between the model predictions of habitat suitability (Fig. 2) and the present-day distribution of *E. verrucosa* (Fig. 1). Firstly, it is logistically and financially expensive to survey all potential areas in which *E. verrucosa* could be present across the UK, so the records database may be incomplete, and the model may have indeed captured some areas which genuinely harbour colonies of pink sea fans. Secondly, although the predictive power of the model was very high, these predictions of habitat suitability could be artefacts of the modelling process (see model limitations section). However, further research could test these two hypotheses by conducting targeted surveys in one or more of the newly identified areas which display the highest probabilities of habitat suitability to find out whether *E. verrucosa* are indeed present or absent at these sites. Thirdly, habitat identified by the model may genuinely be suitable for colonisation, but *E. verrucosa* larvae are unable to disperse to these sites because of low dispersal capacity and/or oceanographic barriers to dispersal (Brown et al. 2003; Holland et al. 2017). Unfortunately, studies of dispersal and connectivity tend to focus on characterising populations for which samples are readily available. Moreover, we envisage that this explanation would be difficult to validate unless a translocation experiment was carried out *in situ* which explored whether fragments of the nearest living colonies could survive in one of the uninhabited sites identified by the model.

For *A. digitatum*, the study area did not represent the northern limit of its range which meant discrepancies between the model predictions of habitat suitability and the present-day distribution were less obvious. However, the model showed that most coastal areas around the Faroe Islands contained suitable habitat. Although no presence points from this location were used to train the model, anecdotal evidence suggests that *A. digitatum* do inhabit coastal waters of the Faroe Islands. Thus, this finding provides additional and independent validation of the performance and reliability of this SDM. Nevertheless, in comparison to the present-day distribution (Fig. 1), the model for *A. digitatum* showed little support for suitable habitat in several areas where *A. digitatum* are known to be present, including a central Celtic Sea offshore site (surveyed by the Joint Nature Conservation Committee) and across the southern North Sea which covered coastal sites in the Netherlands, Germany and Denmark. This discordance between the presence records and the habitat suitability predictions is likely a limitation of the model.

Future habitat suitability with projected sea bottom temperatures

The Maxent model for *E. verrucosa*, re-run with projected minimum sea bottom temperatures for 2050 and 2100 using RCP 4.5 (Fig. 4), revealed subtle but noteworthy differences compared to the present-day predictions of habitat suitability. Based on the raster data acquired for this study, minimum sea bottom temperatures across the study area are projected to increase by a mean average of 0.19^{o}C (-0.94–1.35 ^{o}C) by 2050 and by a mean average of 0.58 ^{o}C (-0.59–2.19 ^{o}C) by 2100 under the RCP 4.5 scenario. The model predicts that a number of additional areas in the Irish Sea and the eastern English Channel will harbour more suitable habitat for *E. verrucosa*. Again, this supports the hypothesis that minimum sea bottom temperatures could indeed be one of the limiting factors that explains why the current range of *E. verrucosa* does not extend into parts of the Irish Sea and the eastern English Channel. If *E. verrucosa* are able to take advantage of projected increases in habitat suitability, this suggests that over the next century this species may colonise more coastal areas of south-west and southern England and Wales, as well as parts of the north of Ireland and western Scotland. However, these predictions do not account for future changes in the other predictor variables (Table 1) used to build the model in this study. Therefore, although projected changes in sea bottom temperatures in 2050 and 2100 may appear to drive expansion of pink sea fan ranges in the UK and Ireland, if other variables also change, such as rock cover (unlikely) or orbital velocity (possible in light of changing global weather patterns, e.g. Hu et al. 2020; Gupta et al. 2021), this may affect the future patterns of habitat suitability presented here (Fig. 4, Fig. S4).

Model limitations

There are two potential limitations that may introduce uncertainty in the SDM predictions. Firstly, there could be survey bias associated with the presence records. For instance, most records of pink sea fans and dead man's fingers on the database are recorded by diver surveys which rarely go beyond depths of 50m even though both species are known to inhabit deeper environments. Deeper records may instead come from technical diving surveys or from bottom trawling surveys where an individual is accidentally caught in the gear. Nevertheless, attempts were made to control for this type of survey bias in the analysis by only selecting a single presence point per raster grid cell. A related limitation to this is that there appears to be much greater sampling effort and records available in the GBIF database for both species from the UK, Ireland and France. Although this may be reflective of genuine absences in the southern North Sea, this may also explain why the Netherlands, Belgium, Germany, and Denmark in particular have very few records for *A. digitatum*. This in turn reduces the number of presence points in the model training set for these areas which may in part explain why the predictions of habitat suitability do not match the present-day distribution of *A. digitatum* in the southern North Sea.

Secondly, there could be one or more predictor variables missing from the model which are key factors for determining the distribution of either species. In *E. verrucosa*, a missing predictor variable could explain why some model predictions of habitat suitability extend beyond the present-day northern range limit, or potentially why in both species some areas have well supported presence records with very low probabilities of habitat suitability. For example, both species are commonly found on shipwrecks, which may have come to rest on an area of seabed that is otherwise unsuitable substrate for colonisation, such as bare sand or mud. These artificial reef-like habitats, for example, HMS Scylla in Whitsand Bay, Cornwall, which lies on a seabed of sand and fine shale, can support small populations of *E. verrucosa* and *A. digitatum* (Hiscock et al. 2010). Therefore, obtaining accurate species data for wrecks to include as a predictor variable may improve the performance of the SDMs. In contrast to missing predictors, the resolution of the raster predictor variables used may also explain why some areas have presence records with very low or zero probability of suitable habitat. For instance, some presence records that were located near the shoreline or within estuaries / inlets fell outside of the extent of the raster data and were subsequently removed due to missing data; this meant that the terrain and environmental conditions for this location were not used to train the model and therefore no predictions of habitat suitability were generated for these locations.

Conclusion

This study built Maxent species distribution models for two coastal temperate octocoral species in the north-east Atlantic, *E. verrucosa* and *A. digitatum*. The optimal model for both species had very high predictive performance and mostly captured areas known to harbour populations in their present-day distribution. These models suggested that topography (depth and slope) and sea bottom temperatures were important predictors of present-day distribution in both species. However, wave orbital velocity and rock cover were also identified as key predictors in *E. verrucosa* compared to *A. digitatum*, suggesting that *E. verrucosa* prefers habitats with more rock cover and adequate movements of ocean currents. The model predictions also showed areas of potentially suitable habitat that are not thought to be currently inhabited, particularly in *E. verrucosa*, where areas beyond its known northern range limit were identified. Moreover, analysis with projected sea bottom temperatures in 2050 and 2100 suggested that some of these uninhabited areas may become more suitable over the next century if minimum sea bottom temperatures in the study area increase.

From a conservation management perspective, these results highlight areas of high habitat suitability which may warrant additional targeted protection by inshore marine reserves. For example, increased protection may be afforded to areas where very high habitat suitability accords with confirmed records of high-density populations of *E. verrucosa* (gorgonian ‘forests’), such as found in several areas of Cornwall and Devon in south-west England. Indeed, *E. verrucosa* ‘forests’ are thought to provide valuable habitat for a number of sessile and mobile species but are under threat from bottom-towed gear and moorings. In addition, colonies of *E. verrucosa* are known to act as an ecological indicator of environmental condition (Pikesley et al.

2016) as detachment, disease and mortality may be linked to human disturbance from bottom-towed gear. In conclusion, the results of this study report the habitat preferences and suitability of the pink sea fan and dead man's fingers and provide insights into how populations of pink sea fans may respond to projected changes in sea temperatures.

References

Araújo MB, Anderson RP, Barbosa AM, Beale CM, Dormann CF, Early R, Garcia RA, Guisan A, Maiorano L, Naimi B, O'Hara RB, Zimmermann NE, Rahbek C. 2019. Standards for distribution models in biodiversity assessments. Science Advances, 5: eaat4858. DOI: 10.1126/sciadv.aat4858.

Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O. 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27: 277-284. DOI: 10.1111/geb.12693.

Bohl CL, Kass JM, Anderson RP. 2019. A new null model approach to quantify performance and significance for ecological niche models of species distributions. *Journal of Biogeography*, 46:1101-1111. DOI: 10.1111/jbi.13573.

Bosch S. 2020. sdmpredictors: species distribution modelling predictor datasets. R package version 0.2.9. URL: https://CRAN.R-project.org/package=sdmpredictors.

Budd GC. 2008. Dead man's fingers (*Alcyonium digitatum*). In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*. Plymouth: Marine Biological Association of the United Kingdom. DOI: 10.17031/marlinsp.1187.1.

Burgos JM, Buhl-Mortensen L, Buhl-Mortensen P, Ólafsdóttir SH, Steingrund P, Ragnarsson SA, Skagseth O. 2020. Predicting the distribution of indicator taxa of vulnerable marine ecosystems in the Arctic and sub-arctic waters of the Nordic Seas. *Frontiers in Marine Science*, 7: 131. DOI: 10.3389/fmars.2020.00131.

Brown J, Carrillo L, Fernand L, Horsburgh KJ, Hill AE, Young EF, Medler KJ. 2003. Observations of the physical structure and seasonal jet-like circulation of the Celtic Sea and St. George's Channel of the Irish Sea. *Continental Shelf Research*, 23:533-561. DOI: 10.1016/S0278-4343(03)00008-6.

Chimienti G. 2020. Vulnerable forests of the pink sea fan *Eunicella verrucosa* in the Mediterranean Sea. *Diversity*, 12: 176. DOI: 10.3390/d12050176.

Conci N, Vargas S, Wörheide G. 2021. The biology and evolution of calcite and aragonite mineralization in Octocorallia. *Frontiers in Ecology and Evolution*, 9:623774. DOI: 10.3389/fevo.2021.623774.

Cowen RK, Sponaugle S. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1:443-466. DOI: 10.1146/annurev.marine.010908.163757.

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40:677-697. DOI: 10.1146/annurev.ecolsys.110308.120159.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of Maxent for ecologists. *Diversity and Distributions*, 17:43-57. DOI: 10.1111/j.1472-4642.2010.00725.x.

Feng X, Park DS, Walker C, Peterson AT, Merow C, Papeş M. 2021. A checklist for maximizing reproducibility of ecological niche models. *Nature Ecology & Evolution*, 3: 1382-1395. DOI: 10.1038/s41559-019-0972-5.

Gazeau F, Parker LM, Comeau S, Gattuso JP, O'Connor WA, Martin S, Pörtner H-O, Ross PM. 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology*, 160:2207-2245. DOI: 10.1007/s00227-013-2219-3.

Georgian SE, Kramer K, Saunders M, Shedd W, Roberts H, Lewis C, Fisher C, Cordes E. 2020. Habitat suitability modelling to predict the spatial distribution of cold-water coral communities affected by the *Deepwater Horizon* oil spill. *Journal of Biogeography*, 47: 1455-1466. DOI: 10.1111/jbi.13844.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8: 993-1009. DOI: 10.1111/j.1461-0248.2005.00792.x.

Gupta AS, Stellema A, Pontes GM, Taschetto AS, Vergés A, Rossie V. 2021. Future changes to the upper ocean Western Boundary Currents across two generations of climate models. *Scientific Reports*, 11:9538. DOI: 10.1038/s41598-021-88934-w.

Hijmans RJ, Philips S, Leathwick J, Elith J. 2020. dismo: species distribution modelling. R package version 1.3-3. URL: https://CRAN.R-project.org/package=dismo.

Hijmans RJ. 2021. raster: geographic data analysis and modelling. R package version 3.4-13. URL: https://CRAN.R-project.org/package=raster.

Hiscock K, Sharrock S, Highfield J, Snelling D. 2010. Colonization of an artificial reef in south-west England—ex-HMS 'Scylla'. *Journal of the Marine Biological Association of the United Kingdom*, 90:69-94. DOI: 10.1017/S0025315409991457.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, 318:5857. DOI: 10.1126/science.1152509.

Holland LP, Jenkins TL, Stevens JR. 2017. Contrasting patterns of population structure and gene flow facilitate exploration of connectivity in two widely distributed temperate octocorals. *Heredity*, 119:35-48. DOI: 10.1038/hdy.2017.14.

Hu S, Sprintall J, Guan C, McPhaden MJ, Wang F, Hu D, Cai W. 2020. Deep-reaching acceleration of global mean ocean circulation over the past two decades. *Sciences Advances*, 6:eaax7727. DOI: 10.1126/sciadv.aax7727.

Kass JM, Anderson RP, Espinosa-Lucas A, Juárez-Jaimes V, Martínez-Salas E, Botello F, Tavera G, Flores-Martínez JJ, Sánchez-Cordero V. 2020. Biotic predictors with phenological information improve range estimates for migrating monarch butterflies in Mexico. *Ecography*, 43:341-352. DOI: 10.1111/ecog.04886.

Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP. 2021. ENMeval 2.0: redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*, 12:1602-1608. DOI: 10.1111/2041-210X.13628.

Lauria V, Garofalo G, Fiorentino F, Massi D, Milisenda G, Piraino S, Russo T, Gristina M. 2017. Species distribution models of two critically endangered deep-sea octocorals reveal fishing impacts on vulnerable marine ecosystems in central Mediterranean Sea. *Scientific Reports*. 7: 8049. DOI: 10.1038/s41598-017-08386-z.

Martin S, Hall-Spencer JM. 2017. Effects of ocean warming and acidification on rhodolith/maërl beds. In: Riosmena-Rodríguez R, Nelson W, Aguirre J. (eds) rhodolith/maërl beds: a global perspective. Coastal Research Library, vol 15. Springer, Cham. DOI: 10.1007/978-3-319-29315-8_3.

Merow C, Smith MJ, Silander JA. 2013. A practical guide to Maxent for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36:1058-1069. DOI: 10.1111/j.1600-0587.2013.07872.x.

Mollica NR, Guo W, Cohen AL, Huang K-F, Foster GL, Donald HK, Solow AR. 2018. Ocean acidification affects coral growth by reducing skeletal density. *PNAS*, 115:1754-1759. DOI: 10.1073/pnas.1712806115.

Morato T, González-Irusta JM, Dominguez-Carrió C, Wei CL, Davies A, Sweetman AK, Taranto GH, *et al*. 2020. Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. *Global Change Biology*, 26: 2181-2202. DOI: 10.1111/gcb.14996.

Munro L, Munro C. 2003. Climate change impact on seafan populations. Reef Research, RR Report 6/2003 RR 08.

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP. 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. DOI: 10.1111/2041-210X.12261.

Naimi B, Hamm Na, Groen TA, Skidmore AK, Toxopeus AG. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography*, 37:191-203. DOI: 10.1111/j.1600-0587.2013.00205.x.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190:231-259. DOI: 10.1016/j.ecolmodel.2005.03.026.

Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. Opening the black box: an open-source release of Maxent. *Ecography*, 40:887-893. DOI: 10.1111/ecog.03049.

Pikesley SK, Godley BJ, Latham H, Richardson PB, Robson LM, Solandt JL, Trundle C, Wood C, Witt MJ. 2016. Pink sea fans (*Eunicella verrucosa*) as indicators of the spatial efficacy of Marine Protected Areas in southwest UK coastal waters. *Marine Policy*, 64: 38-45. DOI: 10.1016/j.marpol.2015.10.010.

Ponti M, Turicchia E, Ferro F, Cerrano C, Abbiati M. 2018. The understorey of gorgonian forests in mesophotic temperate reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28: 1153-1166. DOI: 10.1002/aqc.2928.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Readman JAJ, Hiscock K. 2017. Pink sea fan (*Eunicella verrucosa*). In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*. Plymouth: Marine Biological Association of the United Kingdom. DOI: 10.17031/marlinsp.1121.2.

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, 40:913-929. DOI: 10.1111/ecog.02881.

Sillero N, Barbosa AM. 2020. Common mistakes in ecological niche models. *International Journal of Geographical Information Science*, 35: 213-226. DOI: 10.1080/13658816.2020.1798968.

Sofaer HR, Jarnevich CS, Pearse IS, Smyth RL, Auer S, Cook GL, Edwards TC, Guala GF, Howard TG, Morisette JT, Hamilton H. 2019. Development and delivery of species distribution models to inform decision-making. *BioScience*, 69: 544-557. DOI: 10.1093/biosci/biz045.

Tennekes M. 2018. tmap: thematic Maps in R. *Journal of Statistical Software*, 84:1-39. URL: 10.18637/jss.v084.i06.

Tonga R, Purser A, Guinan J, Unnithan V. 2013. Modeling the habitat suitability for deep-water gorgonian corals based on terrain variables. *Ecological Informatics*, 13: 123-132. DOI: 10.1016/j.ecoinf.2012.07.002.

Veloz SD. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. J*ournal of Biogeography*, 36:2290-2299. DOI: 10.1111/j.1365-2699.2009.02174.x.

Warren DL, Seifert SN. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21:335-342. DOI: 10.1890/10-1171.1.

Wenger SJ, Olden JD. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, 3:260-267. DOI: 10.1111/j.2041-210X.2011.00170.x.

Wilson RJ, Speirs DC, Sabatino A, Heath MR. 2018. A synthetic map of the northwest European Shelf sedimentary environment for applications in marine science. *Earth System Science Data*, 10:109-130. DOI: 10.5194/essd-10-109-2018.

Wood C. 2013. Sea Anemones and Corals of Britain and Ireland. Princeton University Press, 2nd Revised edition. ISBN: 978-0957394636.

Yesson C, Taylor ML, Tittensor DP, Davies AJ, Guinotte J, Baco A, Black J, Hall-Spencer JM, Rogers AD. 2012. Global habitat suitability of cold-water octocorals. *Journal of Biogeography*, 39: 1278-1292. DOI: 10.1111/j.1365-2699.2011.02681.x.

Table 1(on next page)

Summary table of the terrain and environmental variables used as predictors in the species distribution models.

The minimum and maximum values for each predictor are shown for the entire study area, *Eunicella verrucosa* presence points only and *Alcyonium digitatum* presence points only.

Table 1: Summary table of the terrain and environmental variables used as predictors in the species distribution models. The minimum and maximum values for each predictor are shown for the entire study area, *Eunicella verrucosa* presence points only and *Alcyonium digitatum* presence points only.

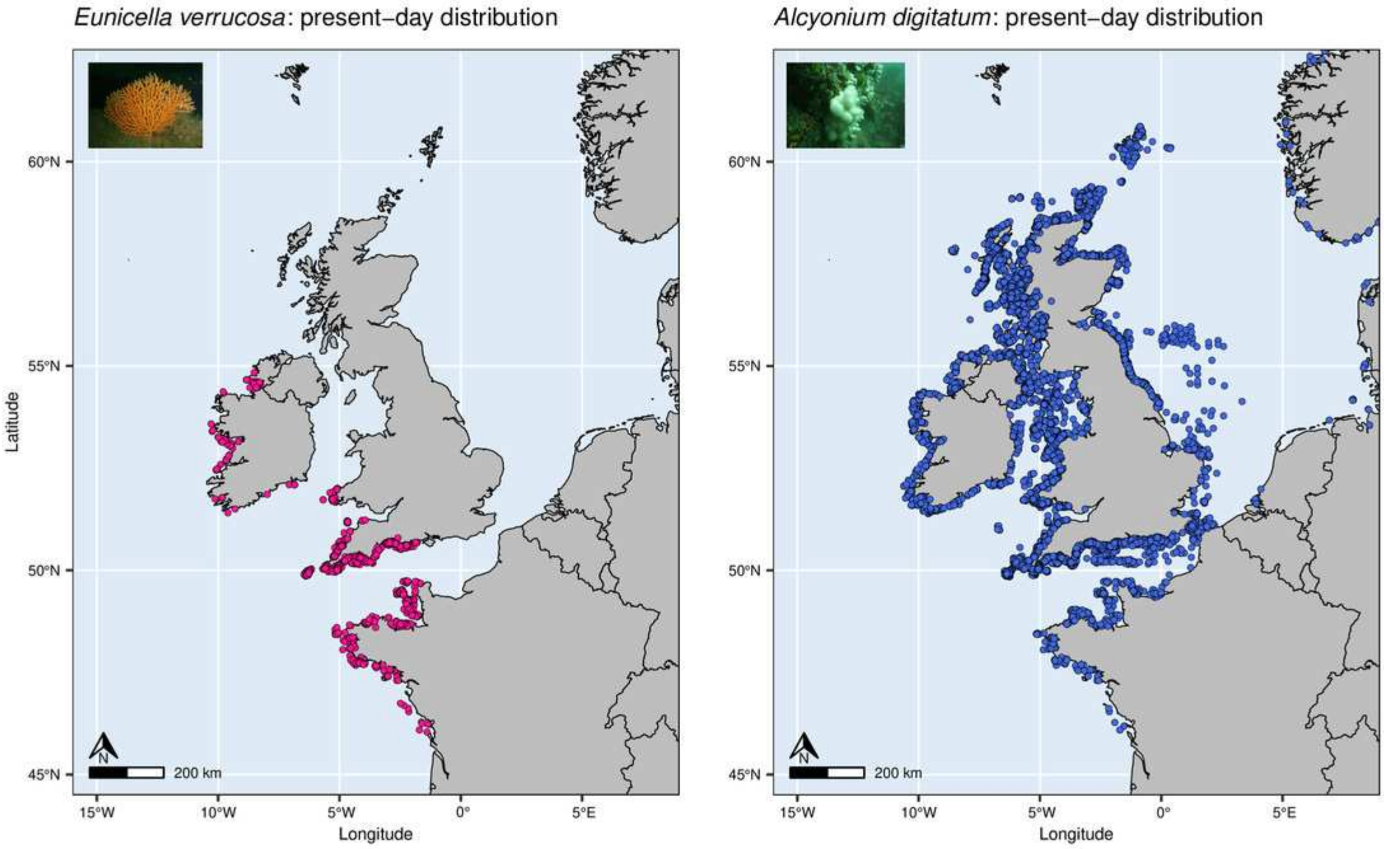
Predictor	**Description**	**Unit**	**Study area (min / max)**	***E. verrucosa*** **(min / max)**	***A. digitatum*** **(min / max)**	**Source**
Terrain						
Bathymetry	Depth of the seafloor	m	1 / 5488	2 / 122	1 / 179	MARSPEC
Slope	Bathymetric slope	degrees	0 / 1.83	0 / 0.10	0 / 0.27	MARSPEC
Rock cover	Fraction of rock in the top 50 cm of sediment	proportion	0 / 1	0 / 1	0 / 1	Wilson et al. 2018
Environmental						
Sea bottom temperature⁺	Minimum sea water temperature at mean bottom depth	°C	-0.91 / 11.27	6.66 / 10.36	0.97 / 9.79	Bio-ORACLE
Orbital velocity	Mean wave orbital velocity at the seabed	ms^{-1}	0 / 1.06	$1.72e^{-2}$ / 0.90	$2.06e^{-4}$ / 0.90	Wilson et al. 2018
Tidal velocity	Mean tidal velocity at the seabed	ms^{-1}	0.09 / 156.82	2.32 / 123.96	2.30 / 136.37	Wilson et al. 2018
Calcite	Mean calcite concentration at sea surface	$mol.m^{-3}$	$5.0e^{-5}$ / 0.060	$1.11e^{-4}$ / 0.023	$5.0e^{-5}$ / 0.050	Bio-ORACLE
pH	pH at sea surface		8.06 / 8.29	8.08 / 8.22	8.06 / 8.26	Bio-ORACLE

⁺Sea surface temperature was excluded from the models due to strong collinearity ($r = 0.97$) with sea bottom temperature.

Figure 1

Present-day distribution of the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*) across the study area.

This area represents the northern range of *E. verrucosa* and the middle-northern range of *A. digitatum* in the north-east Atlantic Ocean. Presence records were extracted from the Global Biodiversity Information Facility data (GBIF) portal on 4th August 2021 (presence data were not available for the Faroe Islands on the GBIF portal but anecdotal evidence supports the presence of *A. digitatum* in the coastal waters of these islands). Image credits: Jamie R. Stevens.



Eunicella verrucosa: present–day distribution

Alcyonium digitatum: present–day distribution

Figure 2

Contribution of each predictor variable to fitting the optimal model.

Proportions for percent contribution and permutation importance are shown for the pink sea fan (*Eunicella verrucosa*) and dead man's fingers (*Alcyonium digitatum*).

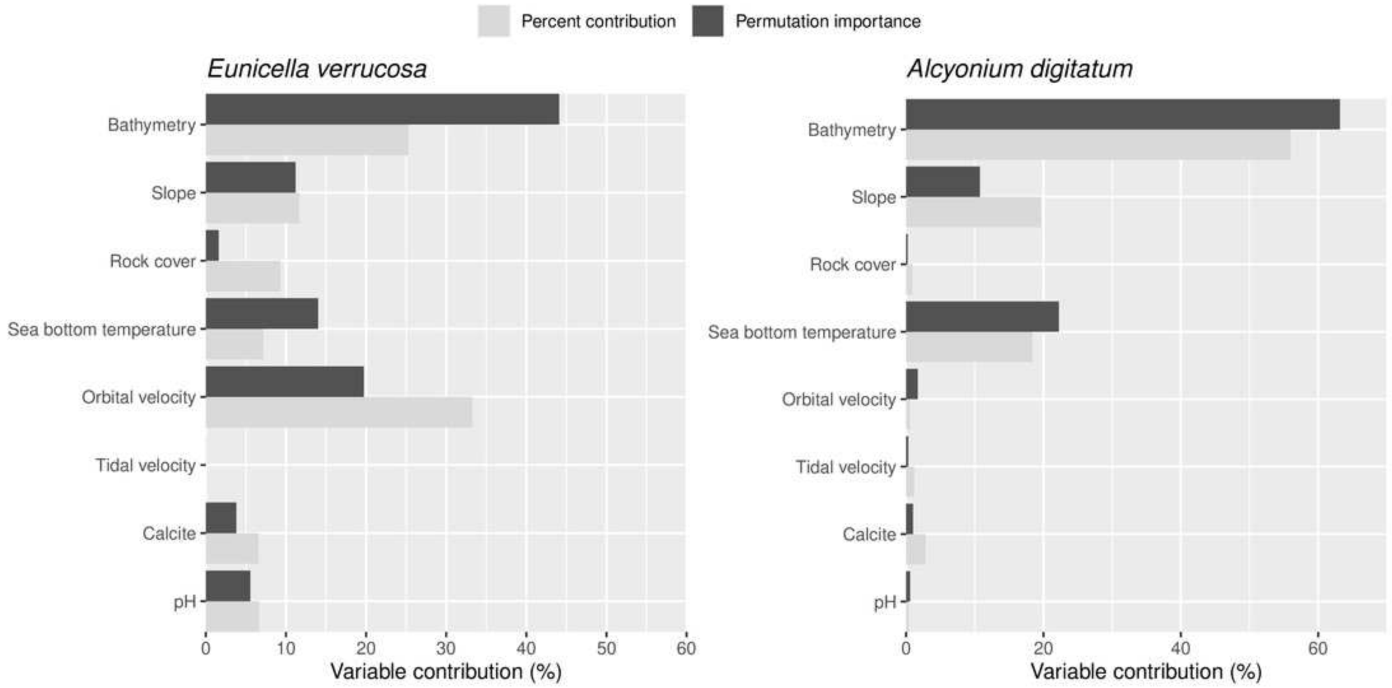


Figure 3

Present-day maps of habitat suitability for the pink sea fan (*Eunicella verrucosa*) and dead man’s fingers (*Alcyonium digitatum*) based on Maxent species distribution models.

Probability of presence is interpreted as a proxy for habitat suitability; only probabilities greater than 0.5 are shown (see Fig. S3 for maps with all probabilities).

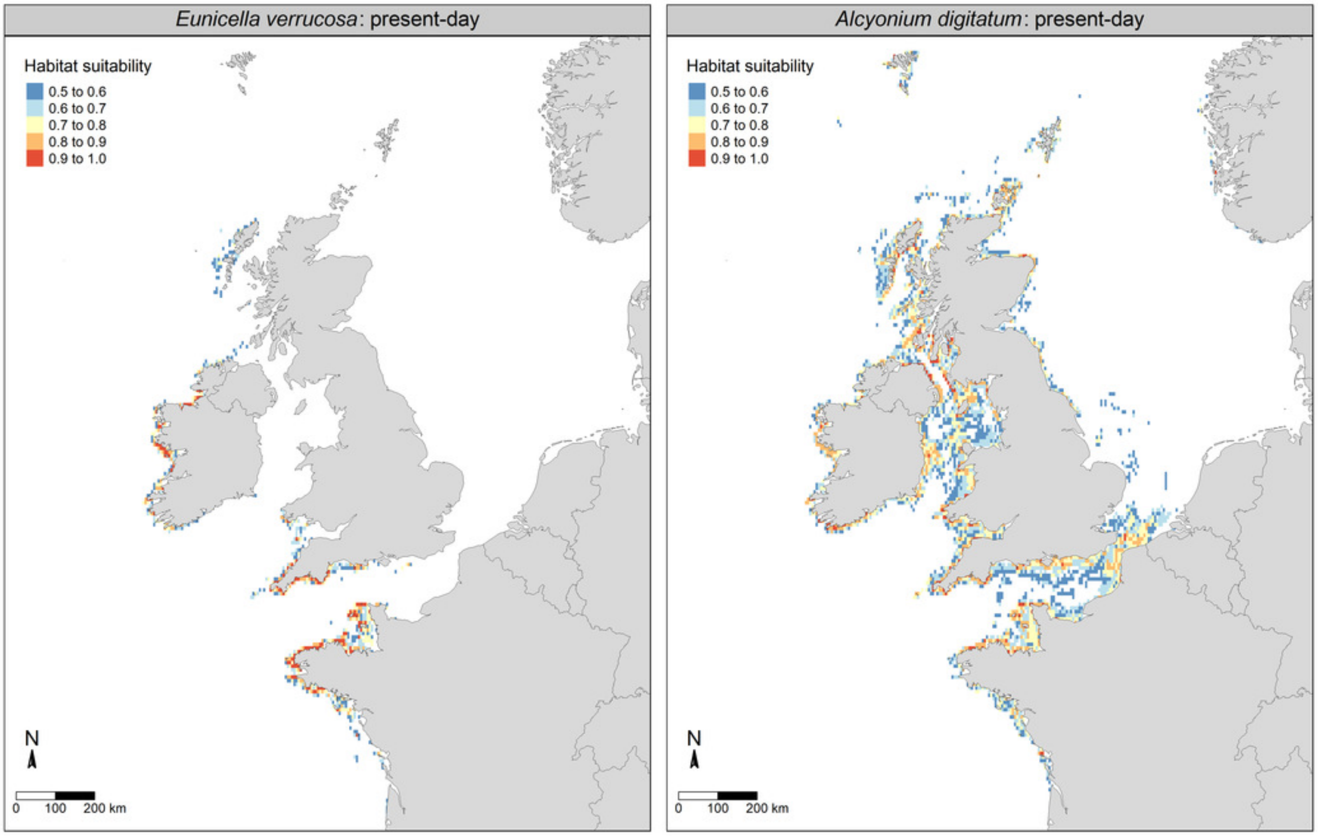
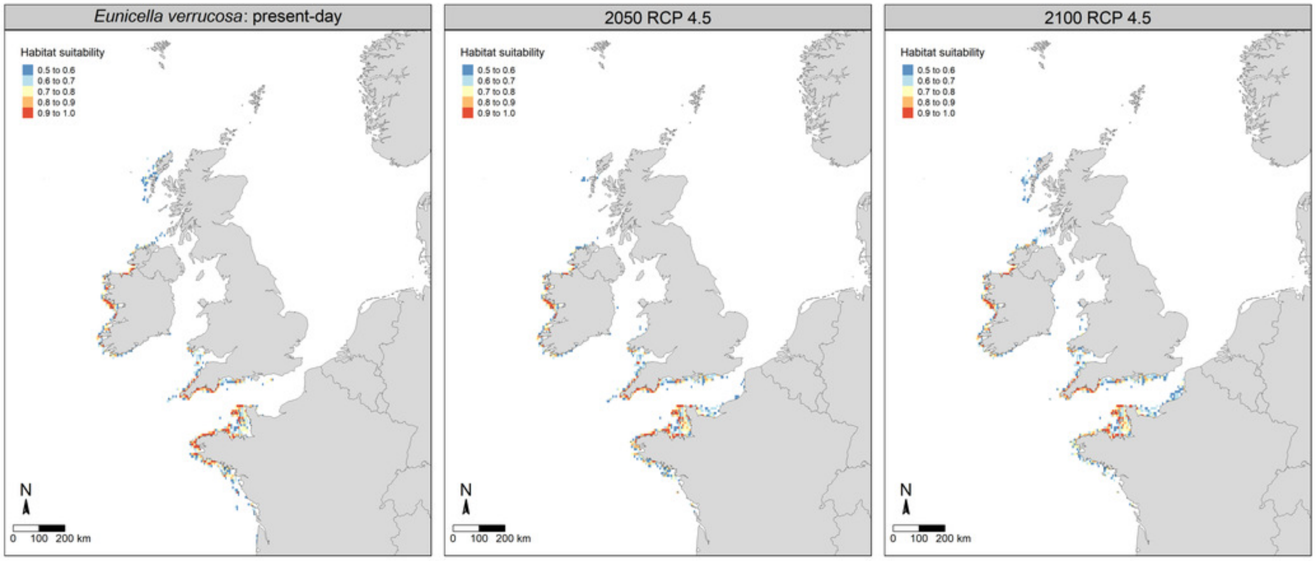


Figure 4

Future predictions of habitat suitability for the pink sea fan (*Eunicella verrucosa*) based on a Maxent species distribution model.

Future layers of sea bottom temperature were substituted for the present-day layer while all other layers used to originally train the model were kept; the model was then re-run to generate future predictions. Predictions for Representative Concentration Pathway (RCP) 4.5 are shown for 2050 and 2100. Probability of presence is interpreted as a proxy for habitat suitability; only probabilities greater than 0.5 are shown.



Eunicella verrucosa: present-day

2050 RCP 4.5

2100 RCP 4.5