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Highlights

- A new habitat modelling open-source framework for non-modeller ecologists.
- An explicit consideration of the third dimension and habitat filter in the modeling procedure.
- An automated procedure for data processing.
- The proposed framework avoids higher projections of species loss.

Abstract

Species Distribution Models (SDMs) are useful tools to project potential future species distributions under climate change scenarios. Despite the ability to run SDMs in recent and reliable tools, there are some misuses and proxies that are widely practiced and rarely addressed together, particularly when dealing with marine species.

In this paper, we propose an open-source framework that includes (i) a procedure for homogenizing occurrence data to reduce the influence of sampling bias, (ii) a procedure for generating pseudo-absences, (iii) a hierarchical-filter approach, (iv) full incorporation of the third dimension by considering climatic variables at multiple depths and (v) building of maps that predict current and potential future ranges of marine species. This framework is available for non-modeller ecologists interested in investigating future species ranges with a user-friendly script. We investigated the robustness of the framework by applying it to marine species of the Eastern English Channel. Projections were built for the middle and the end of this century under RCP2.6 and RCP8.5 scenarios.

Keywords

Bioclimatic envelope models, habitat models, pseudo-absences, vertical gradient, automated modelling framework, future projections

1. Introduction

In a changing world, predicting suitable habitats and potential future species distributions is a central issue in ecology. To this end, Species Distribution Models (SDMs) (also called, depending on the study context, Ecological Niche Models (ENMs), Habitat Suitability Models (HSMs), Habitat Distribution Models (HDMs), Climate Envelope Models (CEM) and other nomenclatures) have been widely used in both terrestrial (e.g. Carboni et al. 2018) and marine realms (e.g. Cheung et al. 2009) to map and predict shifts in species ranges in response to global change, particularly climate change.

We refer here to all models that correlate species occurrences or abundance data with environmental spatial data layers to predict the suitability of any site for a given species. Shifts in species distributions are subsequently projected under different climate change scenarios. These SDMs are correlative and do not incorporate mechanistic information, such as species' physiological response to abiotic conditions.

In the marine realm, there is a flourishing literature carried at global (e.g. Tittensor et al. 2010), regional (e.g. Albouy et al. 2013) and local (e.g. Hattab et al. 2014) scales that have highlighted future species range shift towards the poles (e.g. Morley et al. 2018), deepening (e.g. Pinsky et al. 2013), local extinctions (e.g. Jones & Cheung 2014), habitat fragmentation (e.g. Ben Rais Lasram et al. 2010), species invasions (e.g. Byrne et al. 2016) and impacts on life-history traits (e.g. Genner et al., 2010), on abundances (e.g. Hermant et al., 2010) and on trophic networks (e.g. Doney et al. 2012) due to changing climate in the next few decades.

SDMs have been applied at either the species (e.g. Alabia et al. 2015) or community level (Morley et al. 2018) to assess species vulnerabilities for conservation purposes (Jones et al. 2013) and fisheries management (Asch et al. 2018), and to couple with end-to-end models to simulate spatial patterns of predator-prey interactions (Grüss et al. 2018). Moreover, trophic ecologists are increasingly interested in using SDMs predictions as input for trophic models to investigate how food webs may reorganize due to individual species' responses to climate change (Woodward et al. 2010, Chaalali et al. 2016).

Although SDMs are useful and reliable tools to predict past, present and future species ranges, they rely on strong assumptions and are subject to many uncertainties (Goberville et al. 2015). These uncertainties are well known and occur at every stage of the modelling process (e.g. data collection, choice of algorithms and parameters, model evaluation), but few studies consider them explicitly (Planque 2015, Brun et al. 2020). Moreover, despite the ability to run SDMs in recent, reliable and user-friendly packages and the availability of data in huge global databases (e.g. GBIF, OBIS and FishBase for species occurrences; Bio-ORACLE and MarSpec for environmental variables), there are some misuses and proxies (e.g. data quality, selection of environmental drivers, parametrization, model selection, spatial and temporal scales) that are widely practiced and rarely addressed in the literature (see Jarnevich et al. 2015, Yalcin & Leroux 2017, Duffy & Chown 2017 for examples of reviews and recommendations).

Although global georeferenced data have become more available for both species occurrence/abundance data and environmental variables, less concern has been given to assessing data quality in the marine realm. For example, sampling bias due to diverse and/or non-standardized monitoring surveys may increase the risk of undersampling (e.g. due to selectivity of a sampling method) or oversampling (e.g. in neritic regions or in areas with a long history of monitoring). Consequently, occurrence data often represent a biased sample of species populations, which may significantly alter models calibration (Guillera-Arroita et al. 2015). Careful assessment and pre-processing of data are thus recommended to mitigate effects of sampling bias associated with large-scale occurrence data.

Most studies in the marine realm have been based on two-dimensional SDMs even though species are fundamentally distributed in three dimensions. Duffy & Chown (2017) emphasized the importance of incorporating the third dimension in marine ecological models and showed that ignoring it may influence predictions greatly. Some studies (e.g. Weinmann et al. 2013, Gallardo et al. 2015, Asch et al. 2018) continue to use sea-surface temperature for both pelagic and benthic species despite the temperature gradient between the surface and the bottom.

Moreover, species–environment relationships depend strongly on the scale at which the dependent (i.e. species occurrences) and independent (i.e. environmental data) variables are considered (Cushman & McGarigal 2004). Scale issues are thus important to consider in SDMs especially for the downscaling process (Da Re et al. 2020). It is for example important to choose the appropriate grid size and the relevant variables consistent with the scale at which the ecophysiological processes show greatest

variation (Austin et al. 2011). . The common view is that large-scale processes determine local species diversity, whereas small-scale processes tend to limit the number of species that currently occupy a given site (Pont et al. 2005). To address this issue, a two-stage hierarchical approach based on the concept of "hierarchical filters" is commonly (but not always) used in the terrestrial realm but more rarely in the marine realm (see Heino et al. 2009 and Hattab et al. 2014 for a review of underlying assumptions). In this filtering approach, SDMs are first built at the global scale to consider the full range of climatic conditions (temperature and salinity) species encounters (SDMs can then be termed as Bioclimatic Envelope Models (BEMs)). Then, a habitat filter considering factors at the local scale (such as seafloor type) is applied (the filter can then be termed as Habitat Models (HMs)) . This two-stage approach improves predictions of species distributions at the local scale.
Finally, as policy and decision making require spatially explicit information about the state of and future trends in species ranges, it is useful to generate current and future maps, along with response curves and model performances, for each species.

A broad set of tools exists to model species distribution (e.g. BIOMOD (Thuiller et al. 2009), MAXENT (Phillips et al. 2006), openModeller (de Souza Muñoz et al. 2011), ModEco (Guo & Liu 2010), ENMTool (Warren et al. 2010), sdm (Naimi & Araújo 2016), NPPEN (Beaugrand et al. 2011) and dismo package (Hijmans et al. 2017)). These platforms include a comprehensive set of advanced algorithms that generally need to be supplemented by R scripts to pre-process data or to be coupled with GIS softwares, making them somewhat difficult for non-modeller ecologists to use.

In this paper, we propose a framework that includes (i) a procedure for homogenizing occurrence data to eliminate the influence of sampling bias, (ii) a procedure for generating pseudo-absences, (iii) a hierarchical-filter approach (i.e. global Bioclimatic Envelope Models (BEM) combined with local Habitat Models HM), (iv) full incorporation of the third dimension by considering climatic variables at multiple depths and (v) building of maps that predict current and future ranges of marine species. This framework is available as a ready-to-use R script hosted on GitHub for non-modeller ecologists interested in investigating future species ranges with a user-friendly script.
We investigated the robustness of the framework by applying it to 46 species representing a large part of the biomass in the Eastern English Channel (EEC). Projections were built for the middle and the end of this century under Representative Concentration Pathway (RCP) 2.6 (i.e. rapid mitigation of anthropogenic climate change, optimistic) and RCP8.5 (i.e. business-as-usual, pessimistic) scenarios of the IPCC (Intergovernmental Panel on Climate Change).

2. Model framework

Although designed for the ecosystem of the EEC, our script can be applied to other ecosystems by replacing the habitat data files provided with the script with similar data files for another region. To illustrate application of the script, we considered 46 species representing a large part of the biomass of the EEC (Raoux et al. 2017), with at least 300 occurrences at the global scale and 100 occurrences at a regional scale. We provide the script and environmental data online, at https://github.com/TarekHattab/SDM. For the sake of reproducibility, the script comes with a Docker container (Merkel et al. 2014) including everything needed to run the script. The model framework is described in Figure 2.

2.1 Step 1: Setting global parameters

The script is designed to manage automatically all of the framework's processing steps, described below. Users must set four parameters: (i) species' scientific names, (ii) species' vertical habitats, (iii) the algorithms to be used and (iv) the value of K in K-fold cross-validation.

2.2 Step 2: Data acquisition

2.2.1 Species occurrence data

Species occurrences used in BEMs can be downloaded from five global biogeographic databases:

- Ocean Biogeographic Information System (OBIS): http://www.iobis.org/
- Global Biodiversity Information Facility (GBIF): http://www.gbif.org/

- iNaturalist: http://www.inaturalist.org
- VertNet (vertebrate biodiversity networks): http://vertnet.org/
- Ecoengine (UC Berkeley's Natural History Data): https://ecoengine.berkeley.edu/

Our script cleans the global dataset by deleting erroneous occurrences (e.g. species occurring on land) and occurrences outside a user-defined period. In this study, we deleted records before 1955 and ultimately retained 1 944 154 occurrences from the five databases for the 46 species considered. Additional scientific survey data are available at the regional scale for the EEC and the Bay of Biscay. Thus, the global dataset was supplemented by scientific survey data from IBTS (1990-2016, http://dx.doi.org/10.18142/17), CGFS (1988-2016, http://dx.doi.org/10.18142/11) and EVHOE (1997-2006, http://dx.doi.org/10.18142/8) available from the DATRAS database (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) and also from other surveys of benthic and demersal taxa, such as LANCIE (1997-2002), PECTOW(2001), BENTHOSEINE (1998-1999) and CAMANOC (http://dx.doi.org/10.17600/14001900) (Appendix A). Ultimately, we retained 148 096 occurrences at the regional scale.

2.2.2 Current and projected climatic data

To calibrate BEMs, users can consider temperature and salinity climatologies from the global database WOD 2013 V2 (https://www.nodc.noaa.gov/OC5/woa13/), with a spatial resolution of 0.25°. These climatologies represent mean decadal temperatures and salinities for 1955-1964, 1965-1974, 1975-1984, 1985-1994, 1995-2004 and 2005-2012 for 40 depth layers. These variables were bilinearly interpolated at a $1/12^{th}$-degree spatial resolution (5 arcmin) and aggregated vertically by calculating mean temperature and salinity for the first 50 m of depth to calibrate pelagic species models, for the first 200 m of depth for benthopelagic species models and for the last 50 m of depth for benthic and demersal species models.

For projections, the script performs climate projections for 2041-2050 and 2091-2100 under two RCP2.6 (strong mitigation) and RCP8.5 (business-as-usual) scenarios. These projections are derived from three General Circulation Models (GCMs) of the Coupled Model Intercomparaison Project, Phase 5 (CMIP5) (Taylor et al. 2012): (i) ESM2G (Geophysical Fluid Dynamics Laboratory; NOAA), (ii) CM5A-MR (Institut Pierre-Simon-Laplace) and (iii) ESM-MR (Max-Planck-Institut für Meteorologie). To avoid potential bias of the GCMs compared to historical data, the script calculates anomalies between 2041-2050/2091-2100 and 1955-2012. These anomalies are then added to the observed mean temperatures and salinities for the same period in WOD 2013 data. Current and projected climatic data are provided with the script.

2.2.3 Habitat data

Seafloor type, bathymetry, slope and aspect of the slope (i.e. eastness and northness) are used to build HMs for benthic and demersal species. Data are available from EMODnet Bathymetry (http://www.emodnet-bathymetry.eu/) and EMODnet Seabed Habitats (http://www.emodnet-seabedhabitats.eu/) at a spatial resolution of 250 m. In our study, we aggregated EUNIS seafloor substrate classes into six simplified categories (mud, sand, muddy sand, sandy mud, coarse sediment and gravel). Habitat data grids are provided with the script.

2.3 Step 3: Data pre-processing

Once occurrence data have been downloaded, the script performs a spatiotemporal match between climatologies and occurrence of each species based on geographic coordinates of occurrences and their corresponding decade (to consider climate trends over the past 58 years) and the correct vertical layer, which corresponds to the vertical habitat of the species.

To address the risk of oversampling, and the ensuing over-representation of environmental features (Kramer-Schadt et al. 2013), we first applied an environmental filtering procedure (Beaugrand et al., 2011, Varela et al. 2014) to species occurrences to assign the same weight to over- and under-sampled regions.

To do this, the script creates a grid containing all combinations of temperature and salinity at the global scale for the period 1955-2012 with a resolution of 0.3°C × 0.3 salinity (which represents 100 ×

100 bins). Species occurrences are then projected onto this grid, and only one occurrence is retained in each cell of the grid

The datasets we used were obtained from online databases of occurrences including presence-only data, but the BEMs used in the script require both presence and absence data. The script therefore generates pseudo-absences to better characterize the environmental conditions experienced by a species within the environmental background (Hattab et al. 2014). Pseudo-absences were generated outside the convex hull of presences in the environmental space (Cornwell et al. 2006, Getz & Wilmers 2004). The convex hull was defined as the smallest convex area in the environmental space containing all species records. A restricted convex hull was defined as a convex hull excluding occurrence points in the 1st and 99th percentiles for each environmental parameter in order to exclude observations in the most extreme environmental conditions. Thus, pseudo-absences are randomly selected by the script outside the environmental space described by this restricted convex hull, which is a proxy of the suitable environmental conditions (Figure 1).

In HMs (SDMs used to characterize habitat), pseudo-absences were generated similarly but were based on the "Surface Range Envelope" (Thuiller et al. 2009). In this approach, rectilinear hypervolumes describing the 1st and 99th quantiles of the cells containing presences are used instead of the convex hull. Based on the statistical theory of model-based designs (d-designs; Hengl et al. 2009), the script generates as many pseudo-absences as presences.

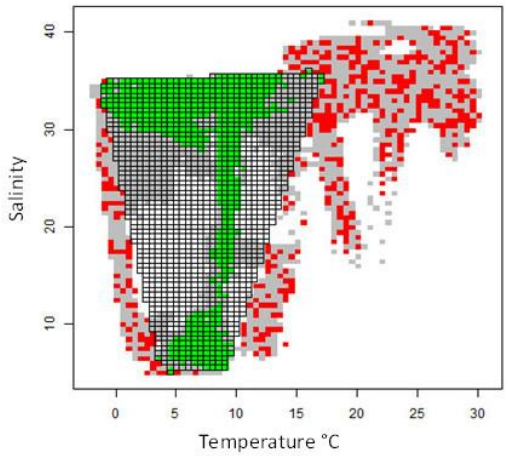

Figure 1. Generation of pseudo-absences. Grey cells represent the environmental space as a combination of temperature and salinity at the global scale. Green cells represent the presence of a given species. The grid represents the restricted convex hull describing the 1st and 99th quantiles of the cells containing presences. Red cells represent pseudo-absences, which are generated randomly outside the convex hull.

2.4 Step 4: Bioclimatic envelope models BEMs

Filtered presence data and the generated pseudo-absences were used to build BEMs that consisted of SDMs applied at the global scale to characterize mainly the bioclimatic envelope of each species according to its temperature and salinity preference. For each species, the script applies eight modelling techniques belonging to four model categories using the BIOMOD multi-model platform (Thuiller et al. 2009): multiple regressions (Generalized Linear Model, Generalized Additive Model, Multiple Adaptive Regression Splines), regression trees (Boosted Regression Tree, Random Forest, Classification Tree Analysis), discriminant analysis (Flexible Discriminant Analysis) and learning techniques (Artificial Neural Network). For each species, the eight models were calibrated using a random sample of the initial data (67%), while the remaining 33% were used to evaluate the model.

Users can perform a 3-fold cross validation procedure and assess model performance using both the True Skill Statistic (TSS; Allouche et al. 2006) and Continuous Boyce Index (CBI; Hirzel et al. 2006). Note that the script uses mean temperature and salinity from the first 50 m of depth to calibrate pelagic species models, from the first 200 m of depth for benthopelagic species models and from the last 50 m of depth for benthic and demersal species models.

For each species, 24 predictions of current climate envelopes (8 algorithms × 3 permutations) were calculated. Only models with CBI > 0.5 for all three permutations were retained (i.e. models that are resilient to occurrence permutations) for projections of future potential bioclimatic envelopes for each species according to RCP2.6 and RCP8.5 scenarios. Finally, the script generates ensemble suitability maps by calculating the mean suitability of the 24 predictions weighted by the CBI to estimate model-based uncertainty (Thuiller et al. 2009). These maps could then be transformed into binary maps using a probability threshold that optimized the TSS. In addition, the script generates uncertainty maps by calculating the standard deviation of predictions.

2.5 Step 5: Habitat models HMs

HMs are SDMs used to characterize local habitat variability. Because habitat variables can be strongly intercorrelated, the script can remove multicollinearity by using the ordination method of Hill & Smith (1976). The resulting orthogonal and uncorrelated principal components are used as predictive variables in the HMs. The HMs, used only for benthic and demersal species, are built using the same method used to develop the BEMs.

2.6 Step 6: Combining BEMs and HMs

For benthic and demersal species, users can extract the predicted bioclimatic envelope for their study area from the projected BEM maps. This represents the first hierarchical filter. Next, the habitat map is used to filter out habitats deemed unsuitable by the HM. The extracted cells can be resampled on a grid (we used one with 250 m resolution) using bilinear interpolation. Thus, an area is considered suitable for a species if both the first filter (BEM) and second filter (HM) predict it as suitable.

2.7 Step 7: Visualizing predictions

The final stage of the framework automatically plots current and future species ranges for both periods (2041-2050 and 2091-2100) under both scenarios (RCP2.6 and RCP8.5) using only BEM for pelagic and benthopelagic species and combined BEM and HM for benthic and demersal species. Maps are plotted in both suitability index and binary format. Response curves, model performances and number of occurrences can also be provided for each species.

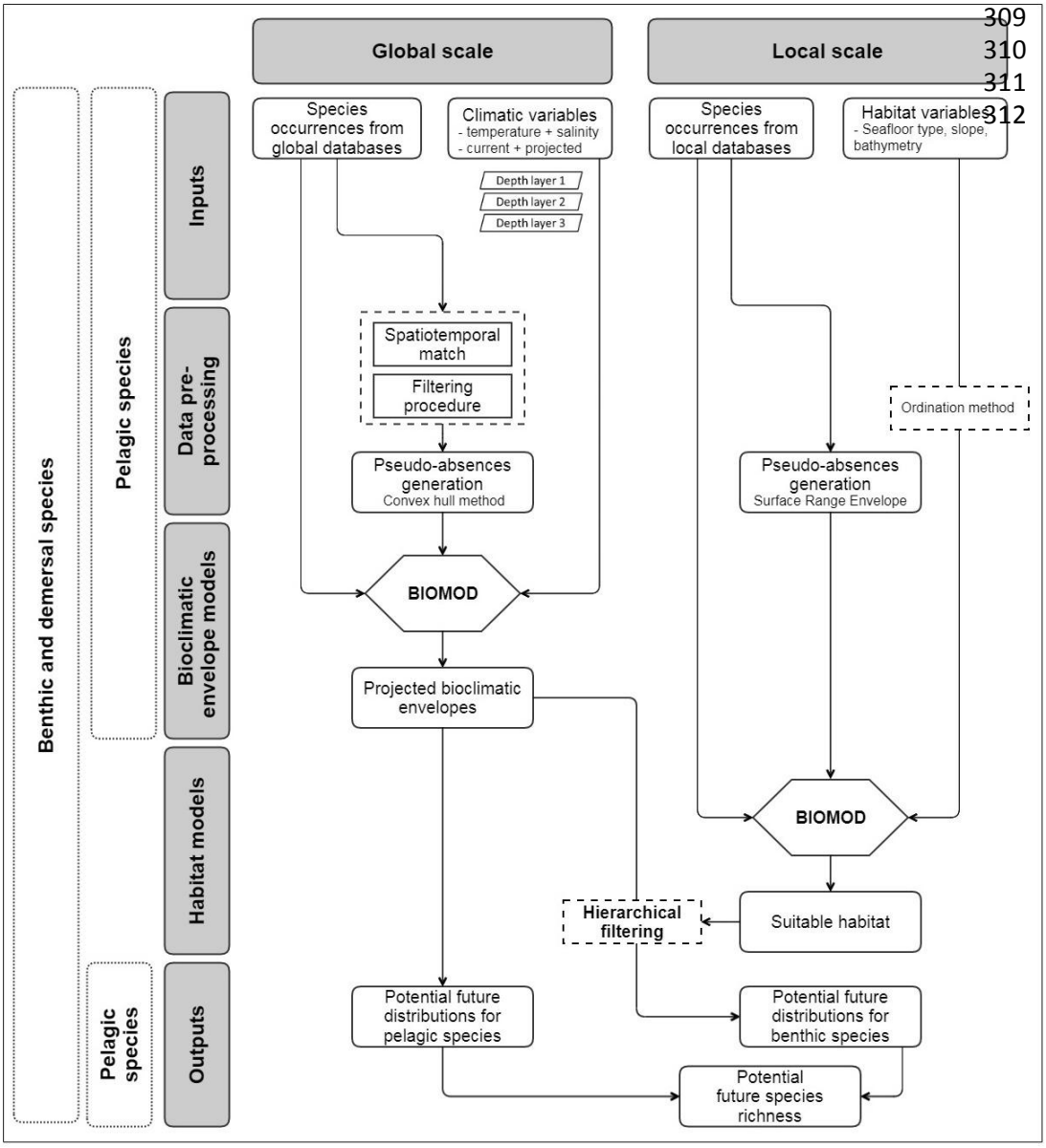

Figure 2. Computational framework and data processing steps

3. Focus on the Eastern English Channel

We applied this modelling framework to the EEC, an epicontinental sea with relatively shallow water (maximum 50 m), subject to a variety of hydrodynamic forces, characterized by a strong tidal range (up to 9 m) and under the influence of river inputs, mainly from the Seine River on the French side (Carpentier et al. 2009) (Figure 3). We considered 46 species that dominate total biomass in the EEC: 15 pelagic and benthopelagic (13 bony fishes and 2 cephalopods), to which we applied BEMs, and 31 benthic and demersal (12 bony fishes, 5 cartilaginous fishes, 6 molluscs, 4 echinoderms, 3 annelids and 1 cnidarian), to which we applied BEMs filtered with HMs (Appendix B).

By the end of the century (2091-2100), the GCMs ESM2G, CM5A-MR and ESM-MR predicted increases in temperature in the EEC of 0.54, 0.79 and 0.73°C, respectively, under RCP2.6 and 1.5, 2.4 and 1.7°C, respectively, under RCP8.5 . For the same period, for ESM2G, CM5A-MR and ESM-MR, salinity anomalies were 0.12, -0.67 and -0.06, respectively, under RCP2.6 and -0.41, -1.45 and -1.11, respectively, under RCP8.5.

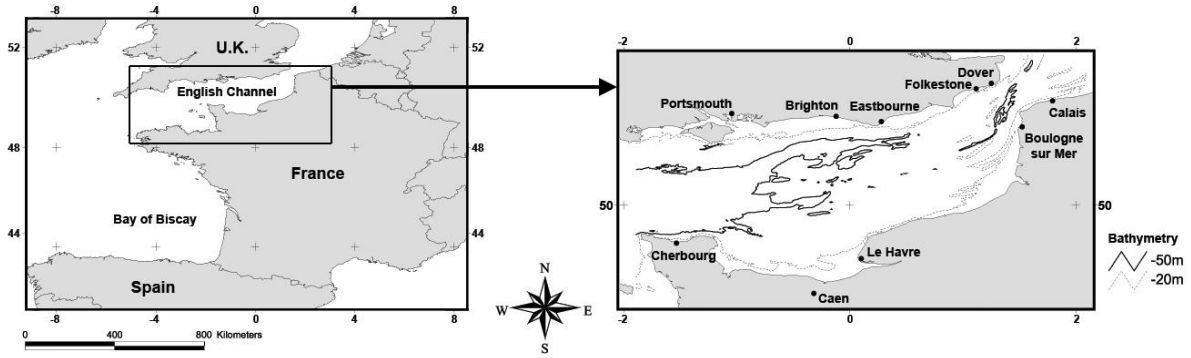

Figure 3. The Eastern English Channel, study area for the application of the script

3.1 Potential changing patterns of species distributions according to the proposed approach

By comparing predictive maps of current species richness to those of future projections in response to changing climate, potential impact of climate change on species' assemblages can be assessed.

Species richness in the EEC currently ranges from 19-46 species. Under RCP2.6, by 2041-2050, species richness was projected to decrease by a mean of 7.8% (i.e. -3.5 species for the entire EEC) and by a maximum of 13.0% (i.e. -6.0 species). The Bay of Seine and the central EEC would lose the most species. Under RCP2.6, by 2091-2100, the decrease would be a mean of 11.5% (i.e. -5.3 species) and a maximum of 19.6% (i.e. -9.0 species). As expected, more species would be lost under RCP8.5, reaching 17.4% of the initial pool by 2041-2050 (-8.0 species) and 54.4% by 2091-2100 (-25.0 species) (Figure 4).

Overall, for both scenarios and both periods, no increase in species range was projected, as none of the species considered was at its northern limit. Species range was projected to be maintained in the EEC for 42 species by 2041-2050 and 39 species by 2091-2100 under RCP2.6 and 41 species by 2041-2050 and 21 species by 2091-2100 under RCP8.5.

Under RCP2.6, by 2041-2050, only three benthic species (the fishes *Pleuronectes platessa* and *Limanda limanda* and the gastropod *Buccinum undatum)* and one benthopelagic species (the fish *Gadus morhua*) were projected to lose 100% of their current range in the EEC (i.e. local extinction). By 2091-2100, two other benthic species (the fish *Platichthys flesus* and the sea urchin *Psammechinus miliaris*) and one benthopelagic species (the fish *Merlangius merlangus*) were projected to lose 50-75% of their ranges.

Under RCP8.5, by 2041-2050, two benthic species (the fish *P. flesus* and the sea star *Asterias rubens*), in addition to those projected to go locally extinct under RCP2.6, were projected to lose 50% and 75% of their ranges, respectively. Under RCP8.5, by 2091-2100, 19 species, both benthic/demersal and pelagic, were projected to go locally extinct.

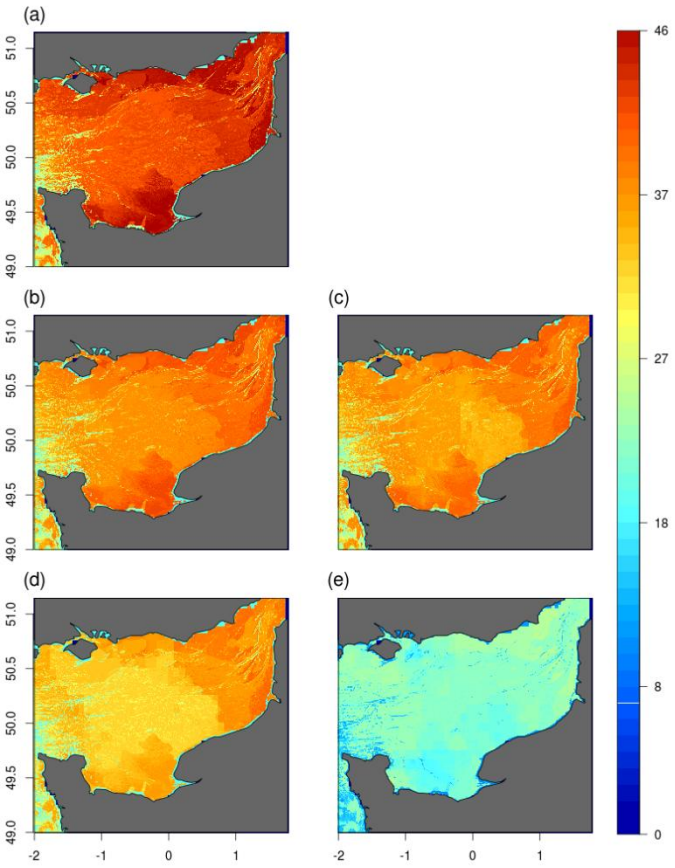

Figure 4. Current and projected species richness in the Eastern English Channel for a pool of the 46 most abundant species. (a) current, (b) projection under RCP2.6 by 2041-2050, (c) projection under RCP2.6 by 2091-2100, (d) projection under RCP8.5 by 2041-2050 and (e) projection under RCP8.5 by 2091-2100.

3.2 Classic approach vs. the proposed framework

According to the complete approach developed in our methodological framework (namely the proposed framework), current species richness was projected to decline by a mean of 3.6% by 2041-2050 and 5.3% by 2091-2100 under RCP2.6 and by 4.4% by 2041-2050 and 16.0% by 2091-2100 under RCP8.5. These rates could be mitigated by the arrival of species that are currently at their northern limit in the English Channel. According to the classic approach (i.e. considering only BEMs and sea surface temperature and salinity), species richness was projected to decline by a mean of 9.3% by 2041-2050 and 6.5% by 2091-2100 under RCP2.6 and by 11.6% by 2041-2050 and 40.8% by 2091-2100 under RCP8.5. Thus, not considering the vertical temperature or salinity gradient or the type of seafloor resulted in higher projections of species loss (Figure 5).

Moreover, considering both scenarios and both periods, the classic approach projected lower range loss (by a mean of 32%) for eight species (mainly benthic or demersal) but projected higher range loss (by a mean of 21%) for 11 species (also mainly benthic or demersal) (Figure 6). The proposed framework and the classic approach yielded similar projections for eight species, mainly benthopelagic (e.g. *Pollachius pollachius*, *Trisopterus minutus*, *Trisopterus luscus*, *Gadus morhua*).

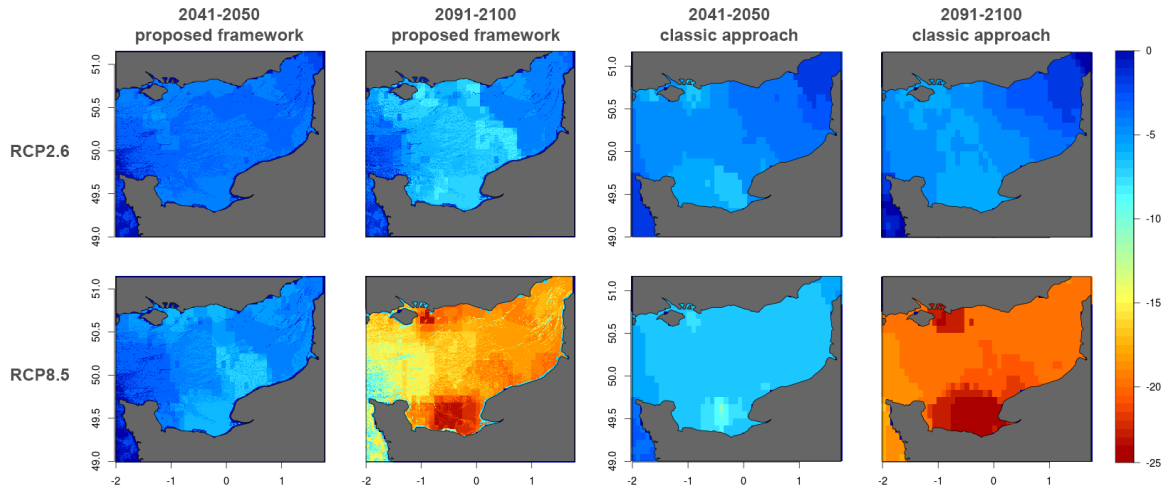

Figure 5. Projected species richness anomalies between current climate conditions and projections for both periods (2041-2050 and 2091-2100), both scenarios (RCP2.6 and RCP8.5) and both approaches (the proposed framework with both vertical climatic conditions and habitat and the classic approach with surface climatic conditions only)

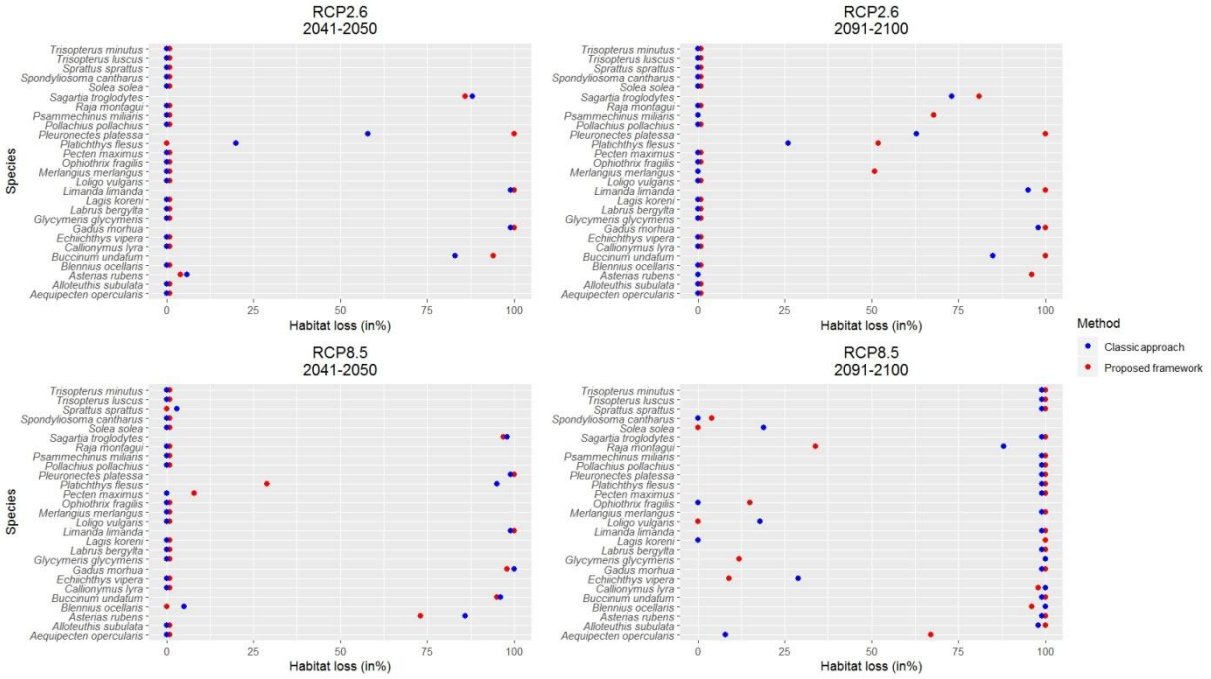

Figure 6. Projected range loss for both periods (2041-2050 and 2091-2100) and both scenarios (RCP2.6 and 8.5) according to the proposed framework (with both vertical climatic conditions and habitat) and the classic approach (with surface climatic conditions only). Plots show species for which a range loss was projected for at least one period, scenario or method.

The framework's projections of the 46 species revealed that the classic approach (i.e. considering only BEMs without vertical climatic conditions or seafloor type) projected higher loss of species richness. In contrast, no general trend was observed in the projected range loss for individual species. Nevertheless, the classic approach may have projected higher range losses more often than it predicted lower range losses, and mainly for benthic or demersal species, which depend on a specific type of seafloor. The classic approach projected range loss of benthic and demersal species due to the loss of suitable temperature conditions at the surface. However, since temperature fluctuates more at the

surface than at the bottom, temperature conditions could remain suitable at the depth range of the species modelled, thus explaining why the classic approach projected higher range losses.
Our results highlight that ignoring the vertical gradient of climatic conditions, even in shallow seas, and the habitat filter leads to inconsistent results. This is even more critical in ecosystems like the EEC that are strongly structured by the seafloor substrate (Dauvin & Desroy 2005, Garcia et al. 2011).

Similar studies exist for marine areas next to the EEC, but none used such a complete framework. Moreover, they are based on the outdated IPCC SRES scenarios and consider only a few species (e.g. only 4 benthic species in the western English Channel; (Rombouts et al. 2012)) or only benthic species (75 benthic species in the North Sea; (Weinert et al. 2016)), making comparison of results difficult.

There are several research perspectives to refine marine species distribution models. Among them, incorporating mechanistic information such as species' physiological response to abiotic conditions (e.g., Feng et al. 2020) is a promising avenue to increase the realism of predicted responses to environmental conditions. In addition, marine species can have complex life cycles with phases that may require distinct models, and thus may be good candidates for infra-specific models (Smith et al. 2018). Another important perspective to consider is the biotic interactions in the process of model building, for example by constructing joint species distribution models.

4. Conclusion

Our results reinforce the need to consider species' positions in the water column and their dependence on a given type of seafloor to avoid biased predictions of species distributions or even misleading results (e.g. Duffy & Chown 2017). In this paper, using the EEC as a case study, we went further and demonstrated that the simple and classic approach that considers sea surface climatic conditions as a proxy of bottom conditions and ignores habitat variables predicts higher species loss.
Species distribution maps are informative, and many atlases contain them. However, they remain descriptive and show only current ranges (e.g. CHARM Atlas of the English Channel; Martin et al. 2009, Carpentier et al. 2009). As assessing species' future distributions is increasingly required for conservation biology and fisheries management, routinely generating maps using a relevant methodological framework would be useful.

We developed a complete and operational framework, from data acquisition and preparation to a two-stage modelling procedure, that considers habitat type, temperature and salinity at species' depth ranges. It creates maps illustrating current and projected ranges as well as response curves for each species. Our script can be adapted for individual needs (e.g., integrating other maps of climatic variables in the same data format) and is suitable for non-modeller ecologists to easily and widely address issues related to changes in species ranges due to climate change.

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Appendix A. Scientific surveys used in this study

Scientific survey	Period	Organisation
IBTS	1992-2015	IFREMER http://dx.doi.org/10.18142/17
CGFS	1989-2016	IFREMER http://dx.doi.org/10.18142/11
EVHOE	1997-2006	IFREMER http://dx.doi.org/10.18142/8
CAMANOC	2014	IFREMER http://dx.doi.org/10.17600/14001900
LANCIE	1997	UMR6143 M2C
PECTOW	1996, 2001, 2006, 2011	UMR6143 M2C
BENTHOSEINE	1998,1999	UMR6143 M2C
BEMACE	2007	UMR6143 M2C
COLMATAGE	2008-2010	UMR6143 M2C
Saint Nicolas		UMR6143 M2C
GEDANOR	2013-2015	UMR6143 M2C
MABEMONO	2006-2007	UMR6143 M2C
ROVMACE	2009	UMR6143 M2C
VDC	2009-2011	UMR6143 M2C
Copale-Authie	1998-2000	UMR6143 M2C

Appendix B. List of species considered in this study. BEM = bioclimatic envelope model, HM = habitat model

Species	Classification	Category in the water column	BEM only	BEM + HM
Limanda limanda	Bony fish	Benthic or demersal		x
Platichthys flesus	Bony fish	Benthic or demersal		x
Pleuronectes platessa	Bony fish	Benthic or demersal		x
Solea solea	Bony fish	Benthic or demersal		x
Blennius ocellaris	Bony fish	Benthic or demersal		x
Callionymus lyra	Bony fish	Benthic or demersal		x
Mullus surmuletus	Bony fish	Benthic or demersal		x
Labrus bergylta	Bony fish	Benthic or demersal		x
Echiichthys vipera	Bony fish	Benthic or demersal		x
Chelidonichthys lucerna	Bony fish	Benthic or demersal		x
Trigloporus lastoviza	Bony fish	Benthic or demersal		x
Dicentrarchus labrax	Bony fish	Benthic or demersal		x
Spondyliosoma cantharus	Bony fish	Benthopelagic	x	
Zeus faber	Bony fish	Benthopelagic	x	
Pollachius pollachius	Bony fish	Benthopelagic	x	
Trisopterus minutus	Bony fish	Benthopelagic	x	
Trisopterus luscus	Bony fish	Benthopelagic	x	
Merlangius merlangus	Bony fish	Benthopelagic	x	
Gadus morhua	Bony fish	Benthopelagic	x	
Clupea harengus	Bony fish	Pelagic	x	
Engraulis encrasicolus	Bony fish	Pelagic	x	
Sprattus sprattus	Bony fish	Pelagic	x	
Sardina pilchardus	Bony fish	Pelagic	x	
Trachurus trachurus	Bony fish	Pelagic	x	
Scomber scombrus	Bony fish	Pelagic	x	
Mustelus mustelus	Cartilaginous fish	Benthic or demersal		x
Scyliorhinus canicula	Cartilaginous fish	Benthic or demersal		x
Scyliorhinus stellaris	Cartilaginous fish	Benthic or demersal		x
Raja clavata	Cartilaginous fish	Benthic or demersal		x
Raja montagui	Cartilaginous fish	Benthic or demersal		x
Lagis koreni	Annelid	Benthic or demersal		x
Lanice conchilega	Annelid	Benthic or demersal		x
Owenia fusiformis	Annelid	Benthic or demersal		x
Pecten maximus	Bivalve mollusc	Benthic or demersal		x

641	*Glycymeris glycymeris*	Bivalve mollusc	Benthic or demersal			x
642	*Aequipecten opercularis*	Bivalve mollusc	Benthic or demersal			x
643	*Ensis directus*	Bivalve mollusc	Benthic or demersal			x
644	*Buccinum undatum*	Gastropod mollusc	Benthic or demersal			x
645	*Sepia officinalis*	Cephalopod mollusc	Benthic or demersal			x
646	*Alloteuthis subulata*	Cephalopod mollusc	Pelagic	x		
647	*Loligo vulgaris*	Cephalopod mollusc	Pelagic	x		
648	*Sagartia troglodytes*	Cnidarian	Benthic or demersal			x
649	*Ophiothrix fragilis*	Echinoderm	Benthic or demersal			x
650	*Echinocardium cordatum*	Echinoderm	Benthic or demersal			x
651	*Psammechinus miliaris*	Echinoderm	Benthic or demersal			x
652	*Asterias rubens*	Echinoderm	Benthic or demersal			x
653						