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Climate change in the Bay of Biscay: Changes in spatial biodiversity patterns could be driven by the arrivals of southern species

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ABSTRACT: Under climate change, future species assemblages will be driven by the movements and poleward shift of local species and the arrival of more thermophilic species from lower latitudes. To evaluate the impacts of climate change on marine communities in the Bay of Biscay, we used the hierarchical filters modelling approach. Models integrated 3 vertical depth layers and considered 2 Intergovernmental Panel on Climate Change (IPCC) scenarios (Representative Concentration Pathway, RCP2.6 and RCP8.5) and 2 periods (2041–2050 and 2091–2100) to simulate potential future species distributions. Results predicted potentially suitable future ranges for 163 species as well as future arrivals of non-indigenous southern species. We aggregated these results to map changes in species assemblages. Results revealed that coastal areas would undergo the highest species loss among the Bay of Biscay species, depending on their vertical habitat (benthic, demersal, benthopelagic or pelagic). Benthic and demersal species were projected to experience a westward shift, which would induce a deepening of those species. In contrast, pelagic species were projected to shift northward. The potential ecological niche for half of the studied species, mostly benthic and demersal, was projected to decrease under climate change. In addition, a high rate of southern species arrivals is expected (+28%). Assessment of community composition showed high species replacement within the 0–50 m isobath, driven by the replacement of native species by southern ones. This could lead to a major reorganization of trophic networks and have socio-economic impacts.

KEY WORDS: Climate change · Ecological niche model · Habitat model · Hierarchical filters · Species turnover · Species distribution

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1. INTRODUCTION

Impacts of climate change on biodiversity have been extensively explored and documented in the literature over the last 2 decades (Harvell et al. 2002, Root et al. 2003, Hoegh-Guldberg & Bruno 2010,

Poloczanska et al. 2013, Pecl et al. 2017, Lenoir et al. 2020). There is now firm evidence that the climate is warming and will continue to warm (Hoegh-Guldberg et al. 2018). In the marine realm, the global upper ocean mean temperature increased by 0.4°C between 1955 and 2008 (Levitus et al. 2009), and global mean

surface temperatures are projected to increase by 1.64 to 3.51°C by the end of the century (Hoegh-Guldberg et al. 2018). Temperature changes impact marine diversity at different levels (Perry 2005, Cheung et al. 2009, Doney et al. 2012), including life history traits (e.g. Genner et al. 2010), abundances (e.g. Hermant et al. 2010), range shifts (e.g. Brander et al. 2003) and, in consequence, the related trophic networks (e.g. Doney et al. 2012, Albouy et al. 2014).

To evaluate climate change impacts on biodiversity and on ecosystem goods and services, species distribution models (SDMs) have become relevant tools (Cheung et al. 2009, Robinson et al. 2017). Marine SDMs can be built at the global (Cheung et al. 2009), regional (Morley et al. 2018) or local (e.g. Guillaumot et al. 2018, Wabnitz et al. 2018) scale. They can be applied to emblematic species (Vestbo et al. 2018), endemic species (Guillaumot et al. 2018) or those of commercial interest (Alabia et al. 2016, Butzin & Pörtner 2016), from corals (Cacciapaglia & van Woesik 2018) to seabirds (Krüger et al. 2018), including copepods (Brun et al. 2016) and fishes (Cheung et al. 2016a). SDMs are useful tools for detecting areas where climate change could deeply impact biodiversity (Jones & Cheung 2015), therefore also allowing an evaluation of the possible implications for fisheries (Weatherdon et al. 2016) or conservation decisions (Vestbo et al. 2018). Most marine SDMs confirm a global poleward shift under climate change (Cheung et al. 2009, Chust et al. 2014, Weatherdon et al. 2016). However, shifts differ depending on the vertical habitat of the species in question. Indeed, in the marine realm, species are distributed in 3 dimensions, and one way in which species respond to rising temperature is deepening (Dulvy et al. 2008, Lenoir & Svenning 2015). Despite the importance of this vertical dimension, the majority of marine SDM studies have only used sea surface environmental layers for both pelagic and benthic species range projections (Duffy & Chown 2017).

Marine fauna spatial responses to climate change are expected to be deepening (Dulvy et al. 2008, Lenoir & Svenning 2015), habitat fragmentation, persistence of species in a climatic trap (Ben Rais Lasram et al. 2010) and poleward shifts (Chust et al. 2014, Guillaumot et al. 2018, Lenoir et al. 2020). Latitudinal shifts would imply the arrival of non-indigenous thermophilic species, leading to a tropicalization of marine communities (Cheung et al. 2012). Tropicalization has already been observed at the global scale, especially in temperate marine ecosystems (Vergés et al. 2014), and at the local scale (Sorte et al. 2010, Bañón et al. 2017, Vasilakopoulos et al. 2017).

The northern Atlantic and its neighbouring seas, the North Sea and Baltic Sea, have been the subject of the development of several SDMs (Gogina et al. 2010, Šiaulyš & Bučas 2012, Bucas et al. 2013). The Bay of Biscay, located on the eastern side of the northern Atlantic, is an area of particular interest due to potential cold species emigration to higher latitudes but also to the arrival of thermophilic species originating from the southern Atlantic. Such outcomes are even more realistic because a temperature increase of 0.2°C decade⁻¹ has been proven for in the upper 200 m layer between 1965 and 2004 (Dulvy et al. 2008, Michel et al. 2009) in the Bay of Biscay. In addition, Hily et al. (2008) showed that some macrobenthic species, common in the south of the Bay of Biscay but unusual in the area as a whole in 1960, are now frequent and more abundant in the north. These potential species range shifts are still more challenging to predict because the Bay of Biscay is France's top fishing area.

In this study, we used the hierarchical filters modelling approach (Hattab et al. 2014) and explicitly considered the vertical gradient of temperature (Ben Rais Lasram et al. 2020) to assess the potential impacts of climate change on the spatial distribution of fish and cephalopod species in the Bay of Biscay. More precisely, we investigated the vulnerability of species to climate change in the periods 2041 to 2050 and 2091 to 2100 under 2 Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway (RCP) scenarios: 2.6 (optimistic) and 8.5 (pessimistic). We also investigated climate-related arrivals from the southern Atlantic. Changes in species richness and composition were analysed together to fully examine the potential effects of climate change on species assemblages.

2. MATERIALS AND METHODS

2.1. Study area

The Bay of Biscay is a large gulf located on the eastern side of the North Atlantic Ocean. It is bordered by the Spanish (43.5° N) and French coasts and by the English Channel in the north (48.3° N) (Fig. 1). The continental shelf is narrow in the south and becomes broader in the north. The total study area was about 80 000 km². As a part of the North Atlantic, Bay of Biscay waters are warmed by the Gulf Stream (Palter 2015). Furthermore, in addition to Atlantic Ocean influences, the Bay of Biscay receives a large quantity of freshwater from French rivers, especially the Loire and Gironde. Consequently, the Bay of Bis-

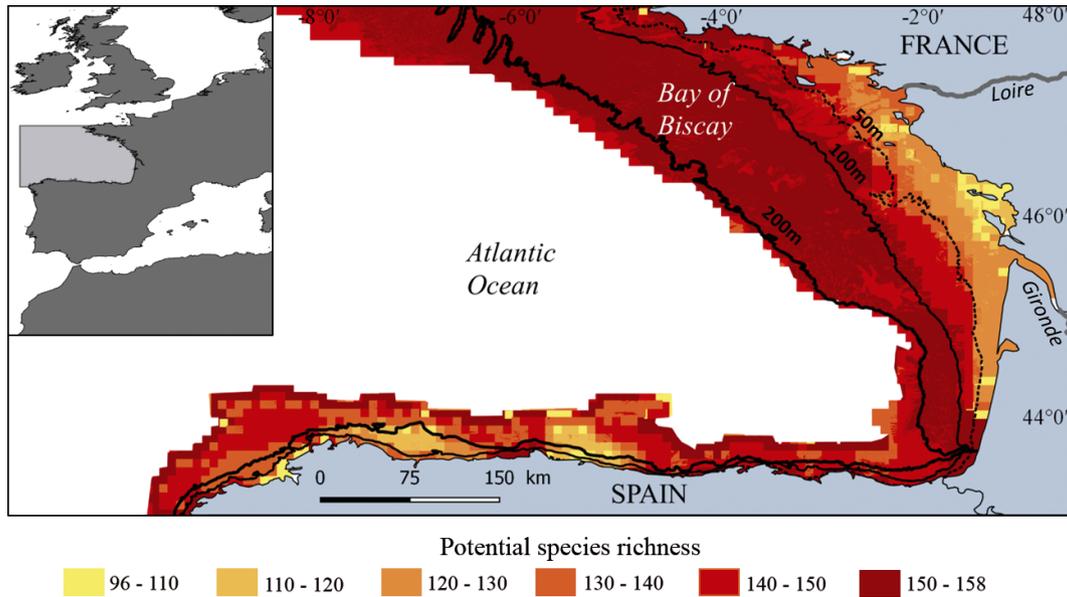


Fig. 1. Current potential species richness in the Bay of Biscay (n = 163 species)

cay is a complex and highly productive area, sustaining a high level of fishing activity (Hily et al. 2008). The main species exploited are sardine *Sardina pilchardus*, hake *Merluccius merluccius*, horse mackerel *Trachurus trachurus*, anchovy *Engraulis encrasicolus* and mackerel *Scomber scombrus* (Moullec et al. 2017).

2.2. Species data

Our modelling procedure requires species data at both global and local scales. Species data at the global scale will be used to fit bioclimatic envelope models (BEMs), and species data at the local scale will be used to fit habitat models (HMs).

A total of 198 coastal fishes and cephalopods, from Brittany to northern Spain, were selected from Ocean Biogeographic Information System (OBIS; www.iobis.org) and Global Biodiversity Information Facility (GBIF; www.gbif.org) databases. This list encompasses about 40% of the fish and cephalopod species of the Bay of Biscay, according to FishBase (www.fishbase.org). We did not model any crustaceans because, apart from some commercially targeted species, their distribution areas are insufficiently known. We also selected 127 species whose northern limits of distribution are found between Spain (43.5°N) and southern Morocco (27.0°N) to project their potential arrival in the Bay of Biscay. For each of these 325 species (198 in the Bay of Biscay and 127 southern), occurrences at the global scale

were uploaded from OBIS, GBIF, iNaturalist (www.inaturalist.org) and VertNet (vertnet.org) databases, as well as from Ecoengine (University of California Berkeley's Natural History Data; <https://ecoengine.berkeley.edu/>). The vertical habitats of the species were then specified according to FishBase: pelagic and benthopelagic species, with no substratum requirements, and benthic and demersal species, with specific substratum requirements. Species with less than 20 occurrences were discarded, leaving 300 species (190 in the Bay of Biscay and 110 in the more southern area delimited by the 27°N latitude) that were used for modelling. To build HMs (applied only to benthic and demersal species) at the local scale, we used occurrences from the Database of Trawl Surveys (DATRAS)–ICES (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx) data sets. We used these data sets because working at the local scale requires a spatial resolution of 300 m or smaller. Occurrences previously downloaded for the first filter were selected to keep only those smaller than 300 m and were combined with those from DATRAS–ICES. All analyses were carried out with R software (v3.6.1) using the script by Ben Rais Lasram et al. (2020) available at <https://github.com/TarekHattab/SDM>.

2.3. Environmental data

The modelling procedure had 2 main steps: a BEM applied at the global scale and calibrated with coarse-

resolution climatic grids, and an HM applied at the local scale and calibrated with fine-grained habitat variables. We selected the 2 extreme scenarios among the set of RCPs to explore the impact of different socio-economic climate policies on climatic projections. RCP8.5 is a high carbon emission, business-as-usual scenario with a net radiative forcing by year 2100 of 8.5 W m^{-2} and a simulated global atmospheric surface temperature change of about $3.7 \pm 0.7^\circ\text{C}$ (mean \pm SD) relative to 1986–2005. RCP2.6 is a strong emission mitigation scenario with a global mean net radiative forcing by year 2100 of 2.6 W m^{-2} and a simulated global atmospheric surface temperature change of about $1.0 \pm 0.4^\circ\text{C}$.

2.3.1. BEM

The BEM was built on the occurrences downloaded for the 300 species at the global scale, to capture the entire bioclimatic niche of each species. To calibrate the BEM, decadal means of temperature and salinity were downloaded from World Ocean Database (WOD) 2013 version 2 for periods between 1955 and 2012 (1955–1964, 1965–1974, 1975–1984, 1985–1994, 1995–2004 and 2005–2012) with a $\frac{1}{4}^\circ$ resolution and divided into 40 depth layers. The data were then interpolated to a 5 arcmin resolution ($\frac{1}{12}^\circ$) using a bilinear interpolation. We aggregated them on the first 50 m depth (pelagic species), first 200 m depth (benthopelagic species), and 50 m from the bottom (benthic and demersal species). Climatic projections for the 2 periods (2041–2050 and 2091–2100) and 2 scenarios (RCP2.6 and RCP8.5) were downloaded from 3 general circulation models (GCMs) from Coupled Model Intercomparison Project Phase 5 (CMIP5): GFDL-ESM2G (NOAA), IPSL-CM5A-MR (Université Pierre et Marie Curie) and MPI-ESM-MR (Max Planck Institut). We considered 2005 to 2012 as a baseline decade and calculated projected anomalies between this baseline decade and 2091 to 2100 and 2041 to 2050. These anomalies were then added to the observed average temperatures and salinities for the same period in the WOD 2013 data.

2.3.2. HM

The HM was built on the occurrences downloaded at the local scale. The habitat was characterized by 5 variables: depth, seafloor type, slope and slope orientation (eastness and northness). These environmental data were downloaded from the studied area

for the species currently present in the Bay of Biscay and from their native range for the southern species. Because habitat variables can be strongly intercorrelated, we removed multicollinearity by using the ordination method of Hill & Smith (1976). The resulting orthogonal and uncorrelated principal components were used as predictive variables in the HM. These data are available from the European Marine Observation and Data Network (EMODnet) (EMODnet Bathymetry [www.emodnet-bathymetry.eu/] and EMODnet Seabed Habitats [www.emodnet-seabedhabitats.eu/]) and have a 250 m spatial resolution. The seafloor type was aggregated into 8 European Nature Information System categories: rock, coarse sediment, sand, sandy mud, muddy sand, fine sand, mud and fine mud. The southern species variables were taken from their native ranges.

2.4. Modeling procedure

2.4.1. BEM

The BEM constituted the first climate filter. To model the bioclimatic envelopes of the species, a spatiotemporal matchup between climatology and species occurrence was realized, taking into account the geographic coordinates of occurrences and their corresponding decade (to remove the climate trends over the past 58 yr) and the correct vertical layer corresponding to the vertical habitat of the focal species. There were 3 vertical layers: the first 50 m depth for pelagic species, the first 200 m depth for benthopelagic species and the last 50 m depth for benthic and demersal species. Thereafter, to account for the risk of oversampling, and consequent overrepresentation of environmental features (Kramer-Schadt et al. 2013), we first homogenized species data sets to assign the same weight to over- and under-sampled regions. To do this, we created a grid encompassing all combinations of temperature and salinity occurring at the global scale for the 1955–2012 period with a resolution of $0.3^\circ\text{C} \times 0.3 \text{ psu}$ (which represents 100×100 bins). Then, species occurrences were overlapped on this grid (according to their temperature and salinity values), and 1 data occurrence was retained when more than 1 observation was made in the crossed intervals of temperature and salinity. This threshold was fixed to eliminate the influence of unbalanced sampling (Schickele et al. 2020).

For each species, 8 algorithms were run individually with the BIOMOD2 R package using the default

settings (Thuiller et al. 2009): generalized linear model (GLM), generalized additive model (GAM), multiple adaptive regression splines (MARS), generalized boosting model (GBM), random forest (RF), classification tree analysis (CTA), flexible discriminant analysis (FDA) and artificial neural network (ANN). These models required both presence and absence data. However, as we downloaded only presence data, our datasets did not contain absences. Thus, we needed to generate pseudo-absences, which was done using the convex hull method (Getz & Wilmers 2004, Cornwell et al. 2006). We defined the convex hull as the smallest surface in the environmental space containing all species records. A restricted convex hull has been defined as a convex hull excluding occurrence points within the 1% and 99% percentiles for each environmental parameter. We used the percentiles to exclude observations in the most extreme environmental conditions. Thus, pseudo-absences were randomly selected outside the environmental space delimited by this restricted convex hull, which is a proxy of suitable climatic conditions. Based on the statistical theory of model-based designs (d-designs; Hengl et al. 2009), we simulated for each species as many pseudo-absences, randomly selected, as the number of occurrences (Hengl et al. 2009; Table S2 in the Supplement at www.int-res.com/articles/suppl/m647p017_supp.pdf). After modelling we evaluated the models for each species with a 3-fold cross-validation procedure using 75% of a random sample of the initial data for calibration and the remaining 25% for validation. We assessed predictive performance of the models using the true skill statistic (TSS) and the continuous Boyce index (CBI). For each species, 24 predictions of the current climate envelopes (8 algorithms \times 3 permutations) can be obtained. Only algorithms with CBI > 0.5 for the 3 permutations (i.e. models resilient to the occurrence permutations) were retained. To generate current and projected binary (presence-absence) outputs, a threshold was used that maximized the TSS score of the 8 algorithms (Thuiller et al. 2009).

2.4.2. HM

The habitat filter was applied only for benthic and demersal species, in the same way as for the BEM, and pseudo-absences were generated based on the surface range envelope (Thuiller et al. 2009). In this approach, we applied rectilinear hypervolumes limiting the 1% and 99% quantiles of cells containing presences instead of the convex hull.

2.5. Model averaging and hierarchical filtering

After validation, we retained 210 species (199 fishes and 11 cephalopods; Table S1 in the Supplement) from the 300 species considered: 163 that occur currently in the Bay of Biscay and 47 southern species (from the area between Morocco and Spain). The selected species were those having algorithms with a CBI value higher than 0.5. Among them, 73 are targeted by fishery activities (www.fishbase.in/search.php). Combined BEM and HM can give markedly different projections for the same dataset, and model evaluations often cannot demonstrate which projection is better (Araújo & New 2007). To overcome these limitations, we used the weighted average consensus method (Thuiller et al. 2009), which accounts for model-based uncertainty. For each grid cell and time period, we calculated a probability of occurrence (W) according to the weight of each model, based on TSS values:

$$W_i^{\text{TSS}} = \frac{\sum_j (\text{TSS}_j \times m_{ji})}{\sum_j \text{TSS}_j} \quad (1)$$

where i is a given grid cell, j is a given model and m_{ji} is the projected probability of occurrence in cell i according to model j . Finally, we resampled maps derived from BEM and HM approaches to obtain the same spatial resolution (the finest one, 250 m). Indeed, habitat variables must be integrated at fine scale (250 m), and there are no bioclimatic maps at this fine scale. Once combined, we considered a species to be present only if both filters, climate and habitat, predicted its presence.

2.6. Changes in species composition

To explore modifications of species assemblages through time, we first calculated the pairwise Jaccard dissimilarity index β_{jac} through time (Albouy et al. 2012):

$$\beta_{jac} = \frac{b+c}{a+b+c} \quad (2)$$

where a is the number of species present in both periods, b is the number of species lost, c is the number of species gained and $a + b$ is the baseline species richness. The pairwise Jaccard dissimilarity index ranges from 0 (the species composition is identical between both baseline and projection) to 1 (it is completely different).

The Jaccard dissimilarity index combines 2 components (Baselga 2010) that are important to understanding climate change impacts on biodiversity at a

given location through time: (1) changes in assemblage composition caused by the loss or gain of species (i.e. the nestedness component of β diversity) and (2) changes in assemblage composition caused by a process of species replacement independent of the species richness variations (i.e. the species turnover component of β diversity, Albouy et al. 2012).

Next, by applying this partition, we calculated both the species replacement (β_{jtu} ; Eq. 3) and the nestedness components (β_{jne} ; Eq. 4) as follows:

$$\beta_{jtu} = \frac{2 \min(b, c)}{a + 2 \min(b, c)} \quad (3)$$

where a , b and c are identical to Eq. (2), \min is the smaller of the 2 values b or c and β_{jne} was calculated by the difference between β_{jac} and β_{jtu} (Baselga 2010):

$$\beta_{jne} = \beta_{jac} - \beta_{jtu} \quad (4)$$

Although β_{jac} , β_{jtu} and β_{jne} can be studied separately, the ratio between β_{jne} and β_{jac} enables an appreciation of the contribution of both the replacement and nestedness components (Dobrovolski et al. 2012):

$$\beta_{ratio} = \frac{\beta_{jne}}{\beta_{jac}} \quad (5)$$

Cells with a $\beta_{ratio} < 0.5$ are dominated by the replacement process, and cells with a $\beta_{ratio} > 0.5$ are dominated by the nestedness process. To represent more informative projections, we simultaneously mapped β_{ratio} values and the changes in species richness with a specific colour range. Hereafter, we will call the pairwise Jaccard dissimilarity index β_{jac} through time the temporal beta diversity (TBD).

3. RESULTS

3.1. Projected environmental data

According to the 3 CMIP5 Earth system models — GFDL, IPSL and MPI — and both RCP scenarios, the annual mean sea surface temperature (SST) and sea bottom temperature (SBT) were projected to increase during the 21st century (Fig. S1). In the middle of the 21st century (2041–2050), the models suggested that, on average, the SST would increase by $0.55 \pm 0.07^\circ\text{C}$ (RCP2.6) and $0.55 \pm 0.09^\circ\text{C}$ (RCP8.5). In the same way, CMIP5 Earth system models suggested that, on average, the SBT would increase by $0.43 \pm 0.12^\circ\text{C}$ (RCP2.6) and $0.44 \pm 0.20^\circ\text{C}$ (RCP8.5). At the end of the 21st century (2091–2100), CMIP5 Earth system models predicted that, on average, the SST would increase by $0.56 \pm 0.10^\circ\text{C}$ (RCP2.6) and $1.56 \pm 0.28^\circ\text{C}$

(RCP8.5). For the SBT, the models suggested, on average, an increase of $0.57 \pm 0.13^\circ\text{C}$ (RCP2.6) and $0.82 \pm 0.49^\circ\text{C}$ (RCP8.5) for the end of the century. The projected increase in mean temperatures was predicted to be highest in the coastal region up to the 50 m isobath, especially close to the Gironde estuary. There was no change in the mean salinity for both periods and both scenarios.

3.2. Model prediction accuracies

Considering only reliable models (i.e. models that are resilient to the occurrence permutations), based on the CBI, we checked their performance using the TSS criterion. For the BEM, the predictive accuracy over all modelling techniques was classified as excellent, with a mean TSS criterion of 0.901 ± 0.035 (Tables S3 & S4). The most accurate model was the RF (mean TSS = 0.930 ± 0.032), and the least accurate was the FDA (mean TSS = 0.857 ± 0.044). Within HMs, the predictive accuracy among all modelling techniques was classified as high, with a mean TSS criterion of 0.708 ± 0.002 (Tables S5 & S6). The most accurate model was the RF (mean TSS = 0.795 ± 0.103), and the least accurate was the GAM (mean TSS = 0.650 ± 0.110).

3.3. Impacts on Bay of Biscay species

By considering 163 species currently present in the Bay of Biscay, we found the current potential species richness per cell (Fig. 1) to range from 96 to 158 species, and we predicted a species richness gradient from the coast to the open sea.

Under the RCP2.6 scenario, mid-century model projections suggested that geographical ranges in the Bay of Biscay would increase for 25 species (15%) and decrease for 59 species (36%). Moreover, by the end of the century, geographical ranges would increase for 4 species (5%) and decrease for 68 species (41%). Under the RCP8.5 scenario, mid-century projections suggested that geographical ranges would increase for 21 species (12%) and decrease for 68 species (41%). By the end of the century, geographical ranges would increase for 6 species (3%) and decrease for 75 species (46%).

Among the 163 modelled Bay of Biscay species, 12 were benthic, 29 were benthopelagic, 83 were demersal and 39 were pelagic. Model outputs revealed different responses for fish and cephalopods according to their vertical habitat (Fig. 2). We projected that

under the RCP2.6 scenario, bottom species (i.e. benthic and demersal, $n = 95$) would be the most negatively impacted: 45 species (47%) and 54 species (56%) would lose range by 2041 to 2050 and 2091 to 2100, respectively. Under the RCP8.5 scenario, 50 bottom species (52%) would lose range by 2041 to 2050, and 56 species (59%) would lose range by 2091 to 2100. Moreover, future ranges of benthic and demersal species seem to shift westward (Fig. 2). In contrast, we projected that pelagic species would be less impacted by climate change. Indeed, under the RCP2.6 scenario, only 2 species (10%) would lose range by the middle of the century and 4 species (5%) by the end of the century. Under the RCP8.5 scenario, 3 pelagic species (17%) would lose range by the middle of the century and 8 species (10%) by the end of the century.

These species seem to undergo a northward shift (Fig. 2). Finally, under the RCP2.6 scenario, 10 benthopelagic species (34%) and 12 (41%) benthopelagic species would lose range by the middle and the end of the century, respectively. Under the RCP8.5 scenario, 11 species (38%) would lose range by 2041 to 2050 and 15 species (51%) by 2091 to 2100.

In our data set, 73 species are targeted by fishing activities in the Bay of Biscay. For the RCP2.6 scenario, 23 of these species (34%) are projected to lose future range by the middle of the century. By the end of the century, 25 species of commercial interest (39%) are projected to lose range in the future. Among these species, the common dab *Limanda limanda*, 1 whiting *Merlangius merlangus*, plaice *Pleuronectes platessa* and Atlantic pollock *Pollachius pollachius* are ex-

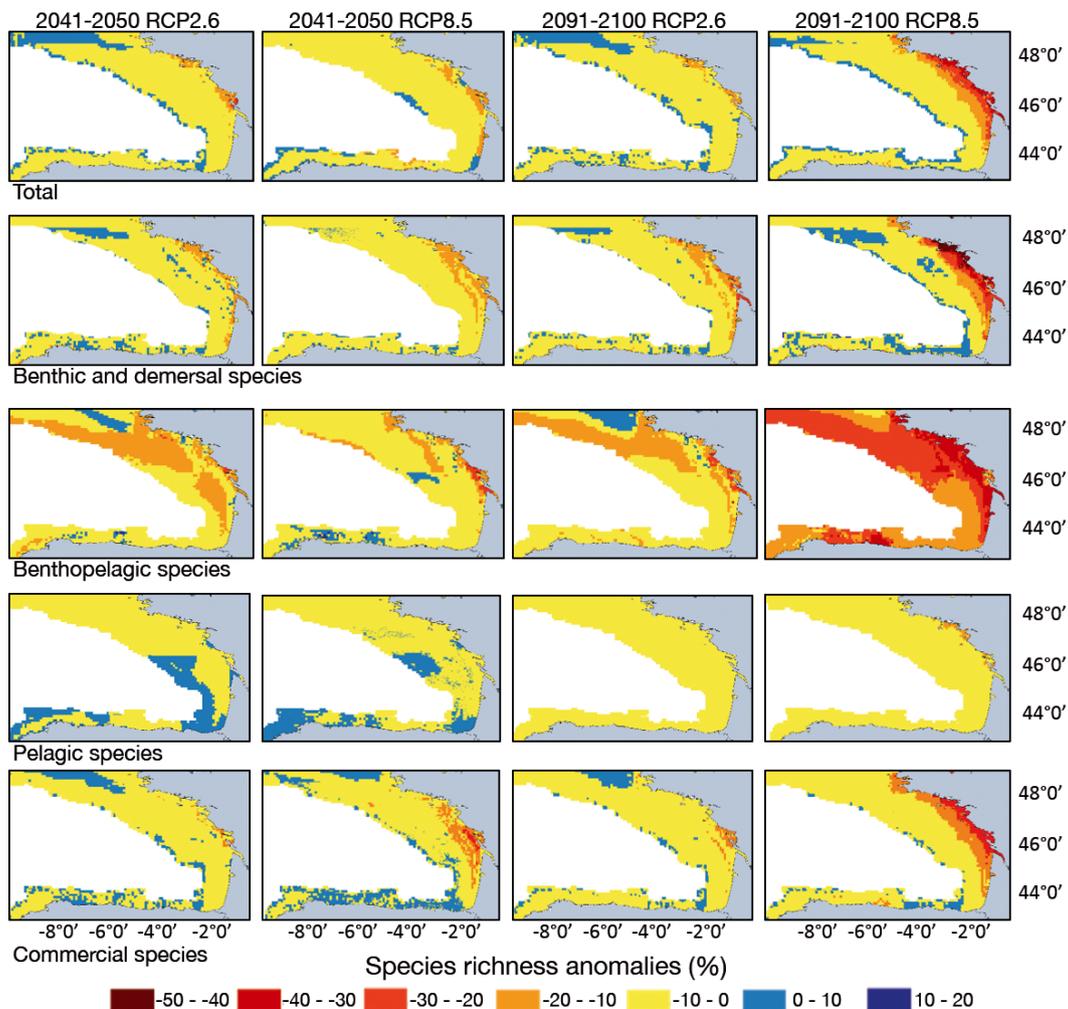


Fig. 2. Projected species richness anomalies (percentage of species richness loss [or gain] between current and future) in the Bay of Biscay for all species ($n = 163$), bottom species ($n = 41$), benthopelagic species ($n = 83$), pelagic species ($n = 39$) and commercial species ($n = 73$) under each scenario and period compared with current species richness. Warm colours represent a decrease in species richness, and cold colours represent an increase in specific richness

pected to lose more than 10% of their current range for the 2 periods. For the RCP8.5 scenario, 26 species (35%) were projected to lose range by mid-century and 30 species (43%) by the end of the century. Some species, like the great sandeel *Hyperoplus lanceolatus*, were projected to gain more than 10% in future range under both scenarios and over the 2 periods. Commercial species were projected to lose suitable habitats in French coastal areas, especially in the Pertuis Charentais marine protected area (Fig. 2).

Model projections indicated a gain in species richness in the north of the Bay of Biscay (Fig. 3). In the studied area as a whole, by the middle of the century (Fig. 3a,b), replacement ($\beta_{\text{ratio}} < 0.5$) would affect a larger area than nestedness under scenarios RCP2.6 (61% of cells) and RCP8.5 (66% of cells). By the end of the century (Fig. 3c,d), nestedness ($\beta_{\text{ratio}} > 0.5$) is dominant under the RCP2.6 scenario (87% of cells) and under the RCP8.5 scenario (86% of cells). Focusing on the different regions close to the French coast, by the middle of the century, a high rate of nestedness combined with a loss of species richness is observed (Fig. 3, red shading). This area with a nest-

edness driven by species richness loss then expands to the entire continental shelf by the end of the century.

3.4. Southern species arrivals

We modelled 47 southern species currently limited to the area between northern Spain and southern Morocco: 8 benthic, 4 benthopelagic, 19 demersal and 16 pelagic species. Among these species, 23 are targeted by fishing activities. Under the RCP2.6 scenario, 33 species (70%) would be expected to expand their future range of distribution to the whole of the Bay of Biscay by mid-century and 35 species (74%) by the end of the century. Under the RCP8.5 scenario, 36 species (77%) would be affected by 2041 to 2050 and 35 species (74%) by 2091 to 2100. Our results highlighted that arrivals of southern species would balance the decrease in species richness in the Bay of Biscay; however, more southern species were modelled to occur over the continental shelf than along the French coast.

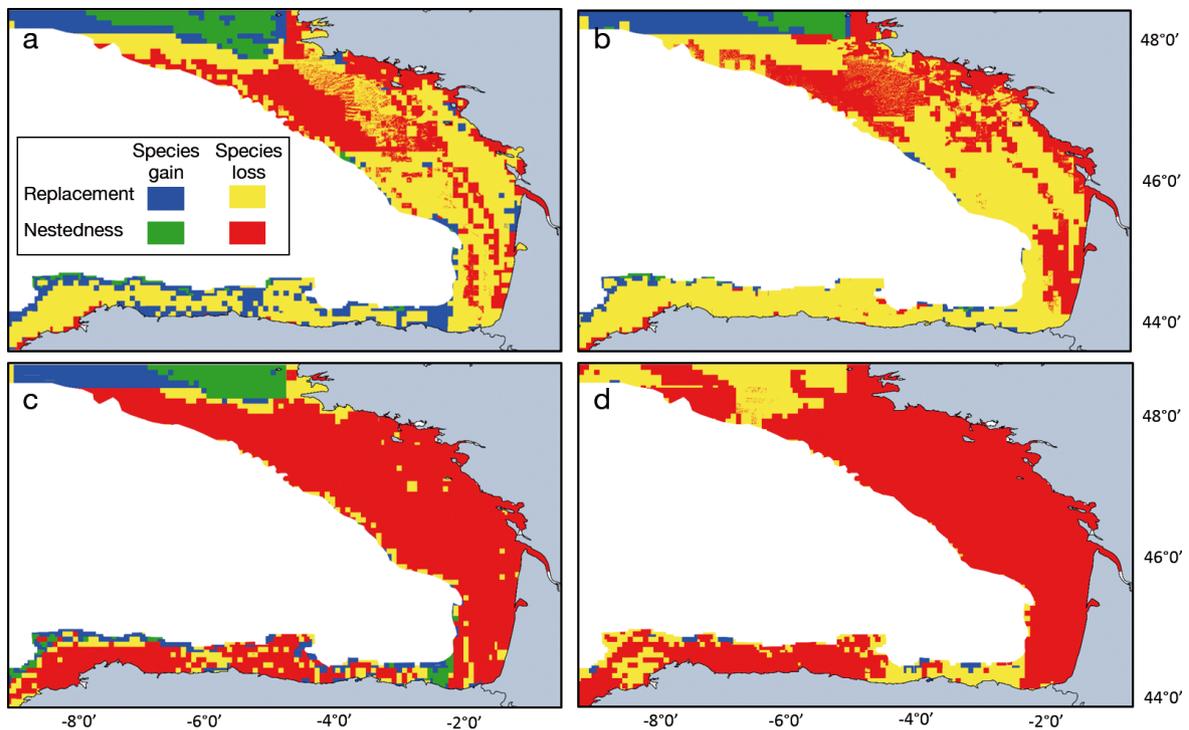


Fig. 3. Changes in species richness and composition considering only the Bay of Biscay species ($n = 163$) calculated for the 2 projected periods, (a,b) 2041–2050 and (c,d) 2091–2100, and the 2 Representative Concentration Pathway (RCP) scenarios, RCP2.6 (a,c) and RCP8.5 (b,d), compared with current species richness. Changes in species composition are quantified using the β_{ratio} index. The 2 colour gradients show the difference in species richness compared with the current situation: cold colours represent cells that would gain species, and warm colours represent cells that would lose species. Blues and yellows indicate the species replacement contribution to the temporal β diversity ($\beta_{\text{ratio}} < 0.5$), whereas greens and reds indicate the species nestedness contribution to the temporal beta diversity ($\beta_{\text{ratio}} > 0.5$)

3.5. Changes in species composition

The species turnover (β_{jtu}) calculated between observed and projected time periods on assemblages including both Bay of Biscay and southern species ($n = 210$) revealed that the highest values occurred close to the French and Spanish coasts (Fig. 4). Under the RCP2.6 scenario, the mean species turnover was

projected to be 28% by mid-century and 30% by the end of the century. Considering the whole studied area under the RCP8.5 scenario, the mean species turnover is expected to be 27% by 2041 to 2050 and 30% by 2091 to 2100. In the whole studied area under the RCP2.6 scenario, 91.4% of the cells would be concerned by nestedness (Fig. 4; $\beta_{ratio} > 0.5$) by 2041 to 2050 and 86.6% by 2091 to 2100. Under the RCP8.5

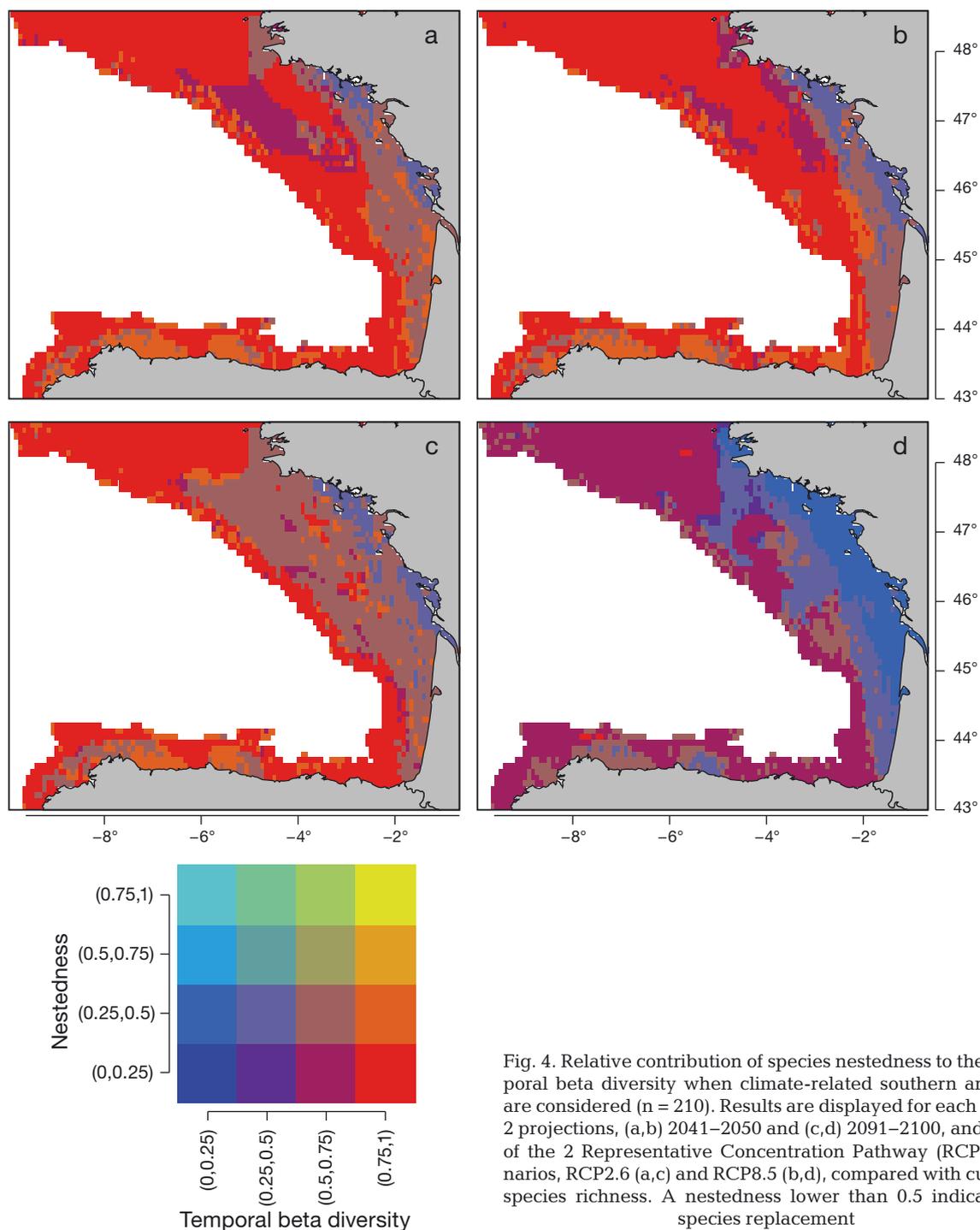


Fig. 4. Relative contribution of species nestedness to the temporal beta diversity when climate-related southern arrivals are considered ($n = 210$). Results are displayed for each of the 2 projections, (a,b) 2041–2050 and (c,d) 2091–2100, and each of the 2 Representative Concentration Pathway (RCP) scenarios, RCP2.6 (a,c) and RCP8.5 (b,d), compared with current species richness. A nestedness lower than 0.5 indicates a species replacement

scenario, 95.8% of the cells would be affected by 2041 to 2050 and 71.7% by 2091 to 2100. Finally, we projected that species replacement would mostly occur in the coastal region up to the 50 m isobath.

4. DISCUSSION

The main goal of this study was to predict future species range shifts likely to occur in the Bay of Biscay under IPCC scenarios RCP2.6 and RCP8.5 by 2041 to 2050 and 2091 to 2100. To achieve this, we applied a methodological framework, combining the hierarchical filters approach (ecological niche model and habitat model).

4.1. Increase in Bay of Biscay temperatures

The averaged projection of the 3 CMIP5 Earth system models highlighted an increase in annual mean temperature of the sea surface and bottom, under both IPCC scenarios and for both periods, in accordance with other studies (Chust et al. 2011, Bruge et al. 2016). It is worth noting that the RCP2.6 and the RCP8.5 scenarios for 2041–2050 both projected very similar increases in SST and SBT, probably due to the influence of the Gulf Stream. Indeed, over the course of the 21st century, we expect a decrease in the strength of the Atlantic meridional overturning circulation, including the Gulf Stream, which would mitigate climate warming by exporting cooler waters to some parts of the North Atlantic (Bryden et al. 2005). Here, the averaged results of the 3 CMIP5 Earth system models suggested that the Bay of Biscay waters may experience a slower warming in the most pessimistic scenario, as observed in other studies (Vellinga & Wood 2002, Gierz et al. 2015). Under both scenarios and for both periods, the maxima of the SST and SBT occurred in the coastal region up to the 50 m isobath. This increase in ocean SST and SBT is expected to have important impacts on ecological systems because temperature is the most important driver explaining shifts in marine species (Pinsky et al. 2013, Cheung et al. 2016a). Salinity was not projected to change from current concentrations.

4.2. Differential impact of climate change on Bay of Biscay species

Our results revealed local changes in species richness in the Bay of Biscay. Projected changes involve

reductions in range size of some species in the bay, coupled with a northward shift. This result is in agreement with other empirical modelling studies that have explored the responses of marine species to climate change scenarios at the global scale (Cheung et al. 2009, Weatherdon et al. 2016).

Bottom species (i.e. benthic and demersal) are expected to be highly impacted by climate change, as already projected for the deep ocean (Brito-Morales et al. 2020). Indeed, over half of these species are likely to experience a reduction of their future potential range, combined with a westward shift. Specifically, models projected a greater decrease of species richness in the coastal region, up to the 50 m isobath, than in the rest of the continental shelf. This shift may be explained by a westward shift to deeper areas where the temperatures are cooler (Dulvy et al. 2008). For example, we modelled a decrease in the extent of the future potential range of the snake pipefish *Entelerus aequoreus* (Fig. S2) that results in a westward shift under the RCP8.5 scenario. Van Damme & Couperus (2008) observed an increase in the abundance of this species in oceanic areas of the northeastern Atlantic since 2004. We also predicted a westward shift for the future potential range of the plaice *Pleuronectes platessa* in the Bay of Biscay under both scenarios and for both periods. The same phenomenon has been noted for this species in the North Sea where the species moved to deeper waters but remained at the same latitude (Perry 2005). Demersal species seemed to undergo both northward and westward shifts, which is similar to previous studies highlighting changes in demersal species communities. For example, Punzón et al. (2016) showed increases in the occurrence of 37 demersal species from the province of Lusitania (Portugal), of which 60% could be explained by temperature increases in intermediate waters in the southern Bay of Biscay. Moreover, the highest decrease in species richness was projected to occur in the inner coastal areas. This is in accordance with a recent study conducted in the Strait of Gibraltar, where demersal species living in shallow waters were observed to be more sensitive to climate variability and tended to experience longitudinal shifts to deeper waters (Delgado et al. 2018).

Our results highlighted that pelagic and benthopelagic species are less impacted by climate change than bottom species. These species are expected to undergo a northward shift (see for example *Merlangius merlangus*, Fig. S3), in accordance with predictions for the Pacific Ocean (Cheung et al. 2015). For example, pelagic fishes of the northeastern Pacific

have been modelled to shift at an average rate of 30.1 ± 2.3 km decade⁻¹ by 2050, which would mean new species arrivals in the Gulf of Alaska and the Bering Sea (Jones & Cheung 2015). In addition, the decrease in species richness could be weaker for pelagic species than for bottom species. The greater impacts of climate change on bottom species than on pelagic species may be explained by the ability of pelagic species to exploit the entire water column. The space limitation of bottom species does not allow them to search for better isotherms. Pelagic species, on the other hand, have more available space. Besides a northward shift, benthopelagic species richness is also projected to greatly decrease in the coastal region up to the 50 m isobath. For example, according to Punzón et al. (2016), *Phycis blennoides* abundances are projected to increase at deeper levels in the south of the Bay of Biscay. Our results corroborate these earlier ones by highlighting a distancing of this species from the French coast for the 2 IPCC scenarios and 2 periods.

For both scenarios and both periods, 60 Bay of Biscay species (36%) were projected to be unaffected by climate change. For these cases, temperature anomalies induced by climate change did not exceed the thermal ranges at which the species occur. These results agree with those from other empirical studies that explored the responses of marine species to climate change (Poloczanska et al. 2013).

The future potential range shifts under different ocean warming scenarios will have effects on the future availability of resources for fisheries (Cheung et al. 2016b). Indeed, among the 73 commercially targeted marine fishes and cephalopods modelled in this study, 29 species would show a northward shift (e.g. *M. merlangus*), a westward shift (e.g. *Microstomus kitt*) or both (e.g. *Pollachius pollachius*). Additionally, climate change is now known to impact suitable spawning areas. For example, the optimal SST for *Engraulis encrasicolus* spawning is around 17°C, and for *Sardina pilchardus*, it ranges from 12 to 15°C (Planque et al. 2007). Consequently, even if ocean warming does not induce a future range shift for these species at the adult stage, it may induce a shift in spawning area and change egg production (Erauskin-Extramiana et al. 2019). In the same way, our results did not reveal a shift of suitable area for *Scomber scombrus*. However, its thermal spawning range shifted northward by 180 km between 1992 and 2013 and is projected to continue this way under RCP8.5 (Brugé et al. 2016). This species is expected to be influenced by climate change, even if its spatial distribution at the adult stage is not impacted.

4.3. Southern species arriving in the Bay of Biscay

The arrival of more thermophilic species from the south would induce a tropicalization of marine communities, an already documented phenomenon over recent decades in the Bay of Biscay. Indeed, Hily et al. (2008) studied the effects of global warming on macrobenthic fauna and concluded that some species, common in the south of the Bay of Biscay in 1960 but unusual in the whole Bay of Biscay, were now more common and abundant in the north. Likewise, the sub-tropical species *Capros aper* (boarfish) was rare in the Bay of Biscay in the 1970s but is now a common species in this area, which can be explained by the increase of sea bottom temperature and by the biology of the species (Blanchard & Vandermeersch 2005). In our study, the potential range of *C. aper* was projected to be maintained over the entire continental shelf, except in the inner coastal areas, for both scenarios and both periods. Moreover, in the Bay of Somme (France), a tropicalization of fish communities has been observed since mid-1990 because of the decrease in abundances of cold-water species (Auber et al. 2017).

The 47 southern species modelled here are expected to experience a northward shift in their future potential range. The arrival of southern species would also lead to trophic interactions with native species, such as competition and predation. For example, trophic competition would occur with the arrival of piscivorous species like bigeye tuna *Thunnus obesus*, Guinean pike conger *Cynoponticus ferox* or pastel ringwrasse *Hologymnosus doliatus*. These new top predators would feed on the prey of native predators, such as *T. alalunga* or *Conger conger*. We also project that *Lagocephalus lagocephalus* (see Fig. S4), a benthopelagic species with flesh toxicity, will show a northward shift in the Bay of Biscay, potentially causing a public health problem (Saoudi et al. 2008). Moreover, in this study, we outlined the shifting of the leading edge of the range for southern species of commercial interest such as Klein's sole *Synapturichthys kleinii*, greater amberjack *Seriola dumerili* and round sardinella *Sardinella aurita*. Moreover, red pandora *Pagellus bellottii* has already been recorded in the southern Bay of Biscay (Iglésias & Lorange 2016). Our results for this species revealed an extension of its future potential range to the entire Bay of Biscay continental shelf for both scenarios and both periods.

Our projections of the arrivals of southern species revealed notable changes in the Bay of Biscay fish and cephalopod assemblages by the middle and end

of the century, under both IPCC scenarios. Indeed, the average TBD in fish and cephalopod assemblages is projected to exceed 25% under both scenarios and for both periods. These rates would reach a maximum of almost 50% in the coastal region up to the 50 m isobath, which is similar to the mean turnover, predicted at over 60% worldwide for 2050 (Cheung et al. 2009).

The measurement of TBD highlighted that changes in biodiversity in projected assemblages in the Bay of Biscay are driven by 2 main processes. The first process is species replacement: species currently present in the area are projected to no longer be there in the future and could be replaced by southern species. The second process is nestedness: some of the species currently present in the area are projected to stay in the future and coexist with southern species (Albouy et al. 2012). Under both scenarios and for both periods, assemblage changes are mainly driven by nestedness, explained by the arrivals of southern species that would coexist with the remaining Bay of Biscay species. However, biodiversity changes along the French coast up to the 50 m isobath are driven by species replacement, because southern species are projected to move into those areas and the native Bay of Biscay species to shift away. This dominance of southern species in French inner coastal areas would induce a tropicalization of current marine communities.

4.4. Potential implications of southern species arrivals

It is noteworthy that because SDMs predict changes in habitat suitability and not changes in the actual distribution per se, there are uncertainties about the arrival of southern species. Indeed, most of the time, the SDM method focuses only on climatic variables and does not take into account biotic species interactions like competition, predation or mutualism (Wisz et al. 2013, Albouy et al. 2014, Fernández & Hamilton 2015). The ecological niche of a species is also delimited by its prey and/or predator distribution areas (Elith & Leathwick 2009) or by a parasite distribution area (Mack et al. 2000). In this study, most of the habitat and environmental conditions (sea temperature and salinity) suitable for southern species already exist in the Bay of Biscay, but such species have not yet been observed because of biotic interactions or abiotic parameters not accounted for in our model (e.g. biogeographical barriers). Consequently, some southern species arrivals projected for the Bay

of Biscay might not occur. Nevertheless, SDM remains a useful tool for predicting future assemblages because temperature is the main driver in marine communities (Dulvy et al. 2008). Furthermore, sea temperature also increases the dimensions of the native areas of many southern species, which would induce a northward shift of the southern limit of their present ecological niche. Moreover, marine species shifts have already been observed on the eastern Atlantic coast (Iglésias & Lorance 2016), which leads us to conclude that our results are reliable.

The southern species studied here cannot be considered as invasive (Urban 2020). However, we cannot exclude that some of them could, in the future, act in the same way as introduced species and cause damage to native communities (e.g. altering ecosystem functions and habitat, reducing native species fitness or causing economic loss [Mack et al. 2000]). Climate change and its consequences have already been seen to benefit invasive species (Walther et al. 2009). On this basis, our results raise questions about the ability of Bay of Biscay fish and cephalopod communities to resist the arrival of new species. In addition to the trophic competition previously discussed, damage caused by invasive species can also be related to the species richness of the new area. Indeed, Elton (2000) suggested that a community's resistance to invaders increases with its species richness. This means that invaders may proliferate not only because of advantageous traits but also because of the lack of predators (Mack et al. 2000). In our case, the potential loss of species richness within the 50 m isobath would lead to empty ecological niches, in which southern species could settle. The lack of predators in such areas could lead to an invasion, with consequences for native species.

4.5. Limits of the approach and perspectives

SDMs are useful and reliable tools to predict past, present and future species ranges, but they are subject to some limits and uncertainties that are well documented in the literature (Goberville et al. 2015, Planque 2016, Yalcin & Leroux 2017). The hierarchical filters approach can, for example, be improved by considering mechanistic information such as the physiological response of species to abiotic conditions (e.g. Feng et al. 2020) or by applying a dispersal filter (Allouche et al. 2008). Here, we focussed on the limits that are specific to the Bay of Biscay. First, for projections, we considered annual mean environmental parameters and did not take into account sea-

sonal variability. Second, some pelagic fishes are migratory and thus are not present in the Bay of Biscay throughout the year. For example, juvenile and pre-adult *T. alalunga* are only present in the Bay of Biscay during summer and early autumn (Sagarmínaga & Arrizabalaga 2010). Third, species occurrences were downloaded from online databases and were therefore not obtained from a well-designed sampling survey, which may have induced an under-representation of non-commercial species, such as those from the family Gobiidae.

Some studies (e.g. Bruge et al. 2016) revealed that thermal niches for spawning of some commercially targeted species would experience a northward shift. For these species at adult stage (e.g. *S. pilchardus*, *S. scombrus*), our results did not project any impact on their future range. Our study could be improved by exploring potential shifts in the ranges of the juvenile stage of species such as *S. scombrus*, *S. pilchardus* and *E. encrasicolus*. Moreover, our modelling approach does not consider a primary productivity filter, which fishes depend on (Cheung et al. 2016a). Finally, genetic plasticity and natural selection, which allow species to adapt to environmental changes, should be taken into account, because they may moderate species shifts. Such phenomena have already been observed in coral reef fishes facing ocean warming and acidification, with results indicating the acclimation and adaptation of some fishes (Rummer & Munday 2017). In addition, human pressures on the environment (e.g. industrial fishing, shipping traffic or ocean acidification) are also an important consideration in the shifts of marine species (Lenoir et al. 2020). Finally, to gain a better understanding of the changes in marine communities induced by climate change, trophic interactions resulting from the new assemblages should be investigated.

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LITERATURE CITED

- Alabia ID, Saitoh SI, Igarashi H, Ishikawa Y and others (2016) Future projected impacts of ocean warming to potential squid habitat in western and central North Pacific. *ICES J Mar Sci* 73:1343–1356
- Albouy C, Guilhaumon F, Araújo MB, Mouillot D, Leprieux F (2012) Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Glob Change Biol* 18:2995–3003
- Albouy C, Velez L, Coll M, Colloca F, Le Loc'h F, Mouillot D, Gravel D (2014) From projected species distribution to food-web structure under climate change. *Glob Change Biol* 20:730–741
- Allouche O, Steinitz O, Rotem D, Rosenfeld A, Kadmon R (2008) Incorporating distance constraints into species distribution models. *J Appl Ecol* 45:599–609
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Auber A, Gohin F, Goascoz N, Schlaich I (2017) Decline of cold-water fish species in the Bay of Somme (English Channel, France) in response to ocean warming. *Estuar Coast Shelf Sci* 189:189–202
- Bañón R, Fernández A, Arronte JC, García D, Villamarín A (2017) New records of two southern fishes found in northern waters of the Iberian Peninsula. *Acta Ichthyol Piscat* 47:401–405
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. *Glob Ecol Biogeogr* 19:134–143
- Ben Rais Lasram F, Guilhaumon F, Albouy C, Somot S, Thuiller W, Mouillot D (2010) The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change: a marine endemic hotspot under threat. *Glob Change Biol* 16:3233–3245
- Ben Rais Lasram F, Hattab T, Nogues Q, Beaugrand G and others (2020) An open-source framework to model present and future marine species distributions at local scale. *Ecol Inform* 59:101130
- Blanchard F, Vandermeirsch F (2005) Warming and exponential abundance increase of the subtropical fish *Capros aper* in the Bay of Biscay (1973–2002). *C R Biol* 328:505–509
- Brander K, Blom G, Fatima Borges M (2003) Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? *ICES Mar Sci Symp* 219:261–270
- Brito-Morales I, Schoeman DS, Molinos JG, Burrows MT and others (2020) Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. *Nat Clim Chang* 10:576–581
- Bruge A, Alvarez P, Fontán A, Cotano U, Chust G (2016) Thermal niche tracking and future distribution of Atlantic mackerel spawning in response to ocean warming. *Front Mar Sci* 3:86
- Brun P, Kiørboe T, Licandro P, Payne MR (2016) The predictive skill of species distribution models for plankton in a changing climate. *Glob Change Biol* 22:3170–3181
- Bryden HL, Longworth HR, Cunningham SA (2005) Slowing of the Atlantic meridional overturning circulation at 25° N. *Nature* 438:655–657
- Bucas M, Bergstrom U, Downie AL, Sundblad G and others (2013) Empirical modelling of benthic species distribution, abundance, and diversity in the Baltic Sea: evaluating the scope for predictive mapping using different modelling approaches. *ICES J Mar Sci* 70:1233–1243
- Butzin M, Pörtner HO (2016) Thermal growth potential of Atlantic cod by the end of the 21st century. *Glob Change Biol* 22:4162–4168
- Cacciapaglia C, van Woesik R (2018) Marine species distribution modelling and the effects of genetic isolation under climate change. *J Biogeogr* 45:154–163
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish* 10:235–251

- Cheung WWL, Meeuwig JJ, Feng M, Harvey E and others (2012) Climate-change induced tropicalisation of marine communities in Western Australia. *Mar Freshw Res* 63: 415–427
- Cheung WWL, Brodeur RD, Okey TA, Pauly D (2015) Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Prog Oceanogr* 130:19–31
- Cheung WWL, Frölicher TL, Asch RG, Jones MC and others (2016a) Building confidence in projections of the responses of living marine resources to climate change. *ICES J Mar Sci* 73:1283–1296
- Cheung WWL, Reygondeau G, Frölicher TL (2016b) Large benefits to marine fisheries of meeting the 1.5°C global warming target. *Science* 354:1591–1594
- Chust G, Borja Á, Caballero A, Irigoien X and others (2011) Climate change impacts on coastal and pelagic environments in the southeastern Bay of Biscay. *Clim Res* 48: 307–332
- Chust G, Castellani C, Licandro P, Ibaibarriaga L, Sagarmina Y, Irigoien X (2014) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J Mar Sci* 71:241–253
- Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465–1471
- Delgado M, Hidalgo M, Puerta P, Sánchez-Leal R, Rueda L, Sobrino I (2018) Concurrent changes in spatial distribution of the demersal community in response to climate variations in the southern Iberian coastal Large Marine Ecosystem. *Mar Ecol Prog Ser* 607:19–36
- Dobrovolski R, Melo AS, Cassemiro FAS, Diniz-Filho JAF (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity: climatic history and beta diversity. *Glob Ecol Biogeogr* 21:191–197
- Doney SC, Ruckelshaus M, Emmett Duffy J, Barry JP and others (2012) Climate change impacts on marine ecosystems. *Annu Rev Mar Sci* 4:11–37
- Duffy GA, Chown SL (2017) Explicitly integrating a third dimension in marine species distribution modelling. *Mar Ecol Prog Ser* 564:1–8
- Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J Appl Ecol* 45:1029–1039
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst* 40:677–697
- Elton CS (2000) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, IL
- Erasquin-Extramiana M, Alvarez P, Arrizabalaga H, Ibaibarriaga L and others (2019) Historical trends and future distribution of anchovy spawning in the Bay of Biscay. *Deep Sea Res II* 159:169–182
- Feng X, Liang Y, Gallardo B, Papeş M (2020) Physiology in ecological niche modeling: using zebra mussel's upper thermal tolerance to refine model predictions through Bayesian analysis. *Ecography* 43:270–282
- Fernández M, Hamilton H (2015) Ecological niche transferability using invasive species as a case study. *PLOS ONE* 10:e0119891
- Genner MJ, Sims DW, Southward AJ, Budd GC and others (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob Change Biol* 16:517–527
- Getz WM, Wilmers CC (2004) A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27:489–505
- Gierz P, Lohmann G, Wei W (2015) Response of Atlantic overturning to future warming in a coupled atmosphere–ocean–ice sheet model. *Geophys Res Lett* 42:6811–6818
- Goberville E, Beaugrand G, Hautekèete NC, Piquot Y, Luczak C (2015) Uncertainties in the projection of species distributions related to general circulation models. *Ecol Evol* 5:1100–1116
- Gogina M, Glockzin M, Zettler ML (2010) Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 2. Modelling and prediction. *J Mar Syst* 80: 57–70
- Guillaumot C, Fabri-Ruiz S, Martin A, Eléaume M, Danis B, Féral JP, Saucède T (2018) Benthic species of the Kerguelen Plateau show contrasting distribution shifts in response to environmental changes. *Ecol Evol* 8:6210–6225
- Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158–2162
- Hattab T, Albouy C, Lasram FBR, Somot S, Le Loc'h F, Leprieur F (2014) Towards a better understanding of potential impacts of climate change on marine species distribution: a multiscale modelling approach. *Glob Ecol Biogeogr* 23: 1417–1429
- Hengl T, Sierdsema H, Radović A, Dilo A (2009) Spatial prediction of species' distributions from occurrence-only records: combining point pattern analysis, ENFA and regression-kriging. *Ecol Modell* 220:3499–3511
- Hermant M, Lobry J, Bonhommeau S, Poulard JC, Le Pape O (2010) Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). *J Sea Res* 64:45–53
- Hill M, Smith A (1976) Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* 25:249–255
- Hily C, Le Loc'h F, Grall J, Glémarec M (2008) Soft bottom macrobenthic communities of North Biscay revisited: long-term evolution under fisheries-climate forcing. *Estuar Coast Shelf Sci* 78:413–425
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* 328: 1523–1528
- Hoegh-Guldberg O, Jacob D, Taylor M, Bindi M and others (2018) Impacts of 1.5°C global warming on natural and human systems. In: Masson-Delmotte V, Zhai P, Pörtner HO, Roberts D and others (eds) *Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. www.ipcc.ch/site/assets/uploads/sites/2/2019/06/SR15_Chapter3_Low_Res.pdf
- Iglésias SP, Lorange P (2016) First record of *Pagellus bellottii* (Teleostei: Sparidae) in the Bay of Biscay, France. *Mar Biodivers Rec* 9:16
- Jones MC, Cheung WWL (2015) Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES J Mar Sci* 72:741–752
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B and others (2013) The importance of correcting for sampling

- bias in MaxEnt species distribution models. *Divers Distrib* 19:1366–1379
- ✦ Krüger L, Ramos JA, Xavier JC, Grémillet D and others (2018) Projected distributions of Southern Ocean albatrosses, petrels and fisheries as a consequence of climatic change. *Ecography* 41:195–208
- ✦ Lenoir J, Svenning JC (2015) Climate-related range shifts — a global multidimensional synthesis and new research directions. *Ecography* 38:15–28
- ✦ Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, Grenouillet G (2020) Species better track climate warming in the oceans than on land. *Nat Ecol Evol* 4:1044–1059
- Levitus S, Antonov JI, Boyer TP, Locarnini RA, Garcia HE, Mishonov AV (2009) Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems: global ocean heat content. *Geophys Res Lett* 36:L07608
- ✦ Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- ✦ Michel S, Vandermeirsch F, Lorance P (2009) Evolution of upper layer temperature in the Bay of Biscay during the last 40 years. *Aquat Living Resour* 22:447–461
- ✦ Morley JW, Selden RL, Latour RJ, Frölicher TL, Seagraves RJ, Pinsky ML (2018) Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLOS ONE* 13:e0196127
- ✦ Moullec F, Gascuel D, Bentorcha K, Guénette S, Robert M (2017) Trophic models: What do we learn about Celtic Sea and Bay of Biscay ecosystems? *J Mar Syst* 172:104–117
- ✦ Palter JB (2015) The role of the Gulf Stream in European climate. *Annu Rev Mar Sci* 7:113–137
- ✦ Pecl GT, Araújo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:eaai9214
- ✦ Perry AL (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- ✦ Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341:1239–1242
- ✦ Planque B (2016) Projecting the future state of marine ecosystems, 'la grande illusion'? *ICES J Mar Sci* 73:204–208
- ✦ Planque B, Bellier E, Lazure P (2007) Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. *Fish Oceanogr* 16:16–30
- ✦ Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. *Nat Clim Chang* 3:919–925
- ✦ Punzón A, Serrano A, Sánchez F, Velasco F, Preciado I, González-Irusta JM, López-López L (2016) Response of a temperate demersal fish community to global warming. *J Mar Syst* 161:1–10
- ✦ Robinson NM, Nelson WA, Costello MJ, Sutherland JE, Lundquist CJ (2017) A systematic review of marine-based species distribution models (SDMs) with recommendations for best practice. *Front Mar Sci* 4:421
- ✦ Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds AJ (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- ✦ Rummer JL, Munday PL (2017) Climate change and the evolution of reef fishes: past and future. *Fish Fish* 18:22–39
- ✦ Sagarminaga Y, Arrizabalaga H (2010) Spatio-temporal distribution of albacore (*Thunnus alalunga*) catches in the northeastern Atlantic: relationship with the thermal environment. *Fish Oceanogr* 19:121–134
- ✦ Saoudi M, Abdelmouleh A, Kammoun W, Ellouze F, Jamoussi K, El Feki A (2008) Toxicity assessment of the puffer fish *Lagocephalus lagocephalus* from the Tunisian coast. *C R Biol* 331:611–616
- ✦ Schickele A, Leroy B, Beaugrand G, Goberville E, Hattab T, Francour P, Raybaud V (2020) Modelling European small pelagic fish distribution: methodological insights. *Ecol Modell* 416:108902
- ✦ Šiaulys A, Bučas M (2012) Species distribution modelling of benthic invertebrates in the south-eastern Baltic Sea. *Baltica* 25:163–170
- ✦ Sorte CJ, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. *Ecology* 91:2198–2204
- ✦ Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* 32:369–373
- ✦ Urban MC (2020) Climate-tracking species are not invasive. *Nat Clim Chang* 10:382–384
- ✦ van Damme CJG, Couperus AS (2008) Mass occurrence of snake pipefish in the northeast Atlantic: result of a change in climate? *J Sea Res* 60:117–125
- ✦ Vasilakopoulos P, Raitzos DE, Tzanatos E, Maravelias CD (2017) Resilience and regime shifts in a marine biodiversity hotspot. *Sci Rep* 7:13647
- ✦ Vellinga M, Wood RA (2002) Global climatic impacts of a collapse of the Atlantic thermohaline circulation. *Clim Change* 54:251–267
- ✦ Vergés A, Steinberg PD, Hay ME, Poore AGB and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc R Soc B* 281:20140846
- ✦ Vestbo S, Obst M, Quevedo Fernandez FJ, Intanai I, Funch P (2018) Present and potential future distributions of Asian horseshoe crabs determine areas for conservation. *Front Mar Sci* 5:164
- ✦ Wabnitz CCC, Lam VWY, Reygondeau G, Teh LCL and others (2018) Climate change impacts on marine biodiversity, fisheries and society in the Arabian Gulf. *PLOS ONE* 13:e0194537
- ✦ Walther GR, Roques A, Hulme PE, Sykes MT and others (2009) Alien species in a warmer world: risks and opportunities. *Trends Ecol Evol* 24:686–693
- ✦ Weatherdon LV, Ota Y, Jones MC, Close DA, Cheung WWL (2016) Projected scenarios for coastal First Nations' fisheries catch potential under climate change: management challenges and opportunities. *PLOS ONE* 11:e0145285
- ✦ Wisz MS, Pottier J, Kissling WD, Pellissier L and others (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol Rev Camb Philos Soc* 88:15–30
- ✦ Yalcin S, Leroux SJ (2017) Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Glob Ecol Biogeogr* 26:609–624