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Impacts of climate change on the Bay of Seine ecosystem: Forcing a spatio- temporal trophic model with predictions from an ecological niche model

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Abstract :

Climate change is already known to cause irreversible impacts on ecosystems that are difficult to accurately predict due to the multiple scales at which it will interact. Predictions at the community level are mainly focused on the future distribution of marine species biomass using ecological niche modelling, which requires extensive efforts concerning the effects that trophic interactions could have on the realized species dynamics. In this study, a set of species distribution models predictions were used to force the spatially-explicit trophic model Ecospace in order to evaluate the potential impacts that two 2,100 climate scenarios, RCP2.6 and RCP8.5, could have on a highly exploited ecosystem, the Bay of Seine (France). Simulations demonstrated that both scenarios would influence the community of the Bay of Seine ecosystem: as expected, more intense changes were predicted with the extreme scenario RCP8.5 than with the RCP2.6 scenario. Under both scenarios, a majority of species underwent a decrease of biomass, although some increased. However, in both cases the stability of the majority of species dynamics was lowered, the sustainability of the fishery. Differences between niche modelling predictions and those obtained through the forcing in Ecospace highlighted the paramount importance of considering trophic interactions in climate change simulations. These results illustrate the requirement of multiplying novel approaches for efficiently forecasting potential impacts of climate change.

Keywords : climate change, ecological niche modelling, Ecospace, fisheries, trophic interactions

1. Introduction

Climate change is now recognized as a threat to the future constitution of marine ecosystems. In the long term its multiple effects are expected to negatively influence biodiversity and ecosystem structure (García Molinos *et al.*, 2016; Wernberg *et al.*, 2016; Poloczanska *et al.*, 2016). Through ocean warming, ocean acidification and oxygen depletion, its consequences are known to influence a multitude of ecosystem services, including fishing provisioning and economic stability (Barange *et al.*, 2014; Weatherdon *et al.*, 2016; Pecl *et al.*, 2017). Therefore, climate change is now increasingly considered in scientific publications concerning marine ecosystems (Haunschild *et al.*, 2016).

Different scenarios exist at the global scale, for example Representative Concentration Pathways (RCP; Moss *et al.*, 2008; Meinshausen *et al.*, 2011) ranging from a drastic reduction in greenhouse gas emissions resulting in limited change in marine systems (i.e. RCP2.6), to business-as-usual emissions resulting in a strong changes in marine systems, such as an increase of several degrees of the average water temperature (i.e. RCP8.5).

The impact of climate change is expected to act at different hierarchical levels of biological organization: organism, population, community and whole ecosystem (Ainsworth *et al.*, 2011; Le Quesne and Pinnegar, 2012; Koenigstein *et al.*, 2016). It is difficult to predict what the consequences of all these will be together, considering the few empirical evidences there has been, and the fact that the initial structure of each ecosystem will influence the aftermath.

Although a few empirical observations of climate change currently exist, ecological models at these different hierarchical levels can be used to more competently forecast the multiple consequences of climate change on marine ecosystems under different scenarios (Hollowed *et al.*, 2009; Stock *et al.*, 2011; Koenigstein *et al.*, 2016). At the species level, climate change effects are often evaluated as predicted distributional shifts, which in turn are estimated as changes in climatic

suitability as predicted by ecological niche models, also known as species distribution models (sensu Hutchinson, 1957; e.g. Cheung *et al.*, 2008, 2009; Hattab *et al.*, 2014). These models (hereafter called SDMs) assume that species will follow the best abiotic ecological niche for themselves, as estimated by abiotic variables such as temperature, salinity or oxygen availability. However, species distributions, especially for higher trophic levels, are also shaped by biotic interactions such as predator or prey distribution (Guisan and Thuiller, 2005; Wisz *et al.*, 2013, Araújo and Rozenfeld, 2014). Thus, SDMs neglect the interplay between climate change and trophic relationships or represent them with simplistic assumptions such as allometric relationships (e.g. Hattab *et al.*, 2016), which in turn can result in a trophic cascade for ecosystem functioning (e.g. Johnson *et al.*, 2011; Luczak *et al.*, 2011; Dalpadado *et al.*, 2012). Contrariwise, models that include trophic relationships in a climate change context rarely consider the spatialization of the individuals, and if they do, it is with a limited amount of species (e.g. Bulman *et al.*, 2006; Field *et al.*, 2006; Cornwall and Eddy, 2015; Chaalali *et al.*, 2016). Therefore, integrating both spatially-explicit climate change predictions on species distributions with trophic relationships represents a major step forward to assess the potential impacts of climate change on entire ecosystems.

In this study, we aim at implementing such an integrated assessment by combining local-scale SDMs of fish with a trophic model for a case study in the French Bay of Seine, which is considered to be one of the most anthropized ecosystems in the world with high marine exploitation (Halpern *et al.*, 2008; Carpentier *et al.*, 2009; Dauvin, 2012). Specifically, we use SDMs to predict future potential fish distributions in 2100 under different climate change scenarios (i.e. RCP2.6 and RCP8.5). These predictions are then used as forcing for a trophodynamic model, Ecospace (Walters *et al.*, 1999; Christensen *et al.*, 2014), in order to investigate the interplay between climate change impacts on species distributions and changes in the trophic food web.

Subsequently, we explore the consequences of the predicted changes in ecosystem functioning for human resource exploitation. Finally, we evaluate the usefulness of such an integrative framework for the forecasting of climate change consequences on marine ecosystems.

2. Material and methods

2.1. Bay of Seine

The Bay of Seine is a shallow coastal area situated in the Eastern English Channel along the French coast and delimited between 49° 25' N and 50° 3' N latitudes, and 1° 3' W and 0° 2' E longitudes. It forms an approximate quadrilateral area of 5000 km², with a mean depth of about 30m. It is an area of high human exploitation, including different fisheries such as netters targeting sole (*Solea solea*) and cod (*Gadus morhua*), beam trawlers targeting sole, bottom otter trawlers targeting cephalopods, cod or whiting (*Merlangius merlangus*), pelagic trawlers targeting european pilchard (*Sardina pilchardus*), black seabream (*Spondylusoma cantharus*) or european seabass (*Dicentrarchus labrax*), and finally dredgers catching king scallop (*Pecten maximus*), one of the most valued fisheries for French and English fishers in the Eastern English Channel. Among the other species harvested, sole and cod are among the most targeted species. In addition to fisheries, the Bay of Seine is also subjected to multiple anthropogenic perturbations such as pollution, transports, sediment dredging and deposition (Dauvin, 2015) as well as offshore windfarm (OWF) projects (Raoux *et al.*, 2017; 2019). Temperature-induced changes were observed through the distribution of benthic invertebrates during the last decades (Gaudin *et al.*, 2018), while projections indicated a reduction of suitable habitat in the area for some of them, even leading to local disappearances (Rombouts *et al.*, 2011).

2.2. Ecospace model of the Bay of Seine

All simulations were based on the model developed by Halouani *et al.* (2020). This model was originally intended to evaluate the potential spillover effect of an OWF in the Bay of Seine ecosystem. To address this question, simulations were conducted through “what if scenarios” evaluation to assess the effectiveness of an exclusion zone inside and bordering the OWF. These scenarios were simulated using a spatio-temporally dynamic Ecospace model, which inherited all the key elements of Ecopath and Ecosim of Bay of Seine (Halouani *et al.*, 2020).

The original Ecopath model comprised 40 trophic groups including plankton, fish, invertebrates, marine mammals and birds (a full description of the model can be found in Halouani *et al.*, 2020; Figures S1-4, Tables S1-7). In addition, two other non-living compartments were included: discards and detritus, as well as six different fishing fleets (nets targeting demersals and crustaceans, pelagic and bottom trawls targeting small pelagics, bottom trawls targeting demersals and cephalopods, pelagic trawls targeting demersals, dredge and other fishing gears).

The Ecopath model is based on the two following mass-balance equations (Christensen and Pauly, 1992):

$$\text{Production} = \text{Predation mortality} + \text{Catches} + \text{Net migration} + \text{Biomass accumulation} + \text{Other mortality} \quad (1)$$

And for each compartment:

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Unassimilated food} \quad (2)$$

The Ecosim model was calibrated over 16 years from 2000 to 2015 (Halouani *et al.*, 2020).

In Ecosim, the dynamics of the different species are obtained by resolving differential equations modelling the biomass evolution of the different trophic groups using the foraging arena theory.

The biomass B_i of a trophic group i evolve using the following formula (Walters *et al.*, 1997):

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \quad (3)$$

Where g_i is the net growth efficiency, Q_{ji} is the consumption rate of the group i , Q_{ij} the cumulated predation undergone by i , I_i the immigration rate, MO_i the non-predation natural mortality, F_i the fishing mortality and e_i the emigration rate.

Ecospace is the spatio-temporal dynamic module of EwE software (Walters *et al.*, 1999). In Ecospace, the same Ecopath and Ecosim differential equations are used in each of the spatial grid cells of the model. In addition, Ecospace has the ability to distribute the biomass of the trophic groups among each grid cell following the interest they have for adjacent cells. This Ecospace feature requires adding a base dispersal rate to the groups. Fisheries are driven by a gravity model, where the fishing effort allocated in each cell is proportional to the sum over groups of biomass x catchability x price of target groups, taking into account the accessibility of areas for fishing activities and the distance between port and fishing ground.

In the original Ecospace model, the Bay of Seine was divided in a grid of 70 rows and 101 columns, each cell being a square of $0.015^\circ \times 0.015^\circ$. The spatial distributions of the trophic groups were driven by sediment type for benthos and depth for the others.

Two major changes were made to the original model presented in Halouani *et al.* (2020). First, we modified the base dispersal rates according to literature to stabilize the long-term Ecospace simulations, according to the environment and speed of species/groups obtained in fishbase (detailed in Table S8). Second, we modified the vulnerability for the predator group ‘Fish poor cod’ on all its prey because its calibrated value was 786.1 (unitless), which is far above the other high trophic levels groups’ vulnerabilities, which was creating extreme fluctuations of biomass in the simulations. Thus, we set it to 2, the original vulnerability value. We compared the change it induced for the fit to time series with the initial fit and it was negligible (sum of squares of 125.605 compared to the previous value of 125.731, starting from an initial value of 5537.832 for default

vulnerabilities), indicating its low importance for the global fit to the time series and thus the lower confidence for its initial value.

Prebalancing analysis (PREBAL; Link, 2010; Darwall *et al.*, 2010; Lassalle *et al.*, 2014, Bentley *et al.*, 2018) were done and didn't demonstrate any major impediment (Table S11, Figures S5-7).

2.3. Species distribution models and climate scenarios

Based on the same approach described by Ben Rais Lasram *et al.* (2020), maps of suitability index were created for 28 of the groups modeled in Ecospace. This was achieved through the coupling of climate projections, derived from three general circulation models, and habitat modelling, with a hierarchical approach where bioclimatic envelop modelling was acting as a first filter and the habitat as a second one, with species occurrences obtained from 5 global biogeographic databases. Maps were modeled for a total of 44 species (Table 1). To decide which species distribution could be determined by ecological niche models, a criterion of 300 occurrences on the Atlantic coast and 100 occurrences in the English Channel had to be met. Lower trophic level groups, as well as birds and marine mammals were excluded from the approach as they cannot be modelled like fish and invertebrates in respect of their adaptation to new conditions. Pelagic and benthopelagic species were modelled using only bioclimatic envelope models while benthic and demersal species were modelled using bioclimatic envelope models filtered by habitat models (Table 1). The baseline scenario we used was based on the current species distributions, while we developed Representative Concentration Pathways (RCPs) scenarios to project potential future species distributions. While other RCP scenarios (RCP4.5 and RCP6) exist, only RCP2.6 and RCP8.5 were tested because they represent the two extremes of the possible changes in future anthropogenic greenhouse gas emissions and should provide the thresholds of plausible ecosystem evolution.

The habitat modelling concerned 30 species among the 44 modeled ones: benthic invertebrates and fish, as well as demersal fish known to be highly influenced by habitat type. Five habitat parameters were used to predict the suitability index of the species: bathymetry, slope, northness, eastness and seafloor type (i.e. coarse sediment, fine mud, fine sand, mud, muddy sand, rock, sand, sandy mud, sediment). We refer readers to Ben Rais Lasram *et al.* (2020) for full methodological details.

2.4. Forcing species spatial distributions in Ecospace

We used the species spatial distributions obtained from niche modelling as two different levers in Ecospace simulations: i) as a proxy of the relative change in biomass and ii) as a representation of the new habitat capacities (i.e. the individual responses of functional groups to environmental conditions; Christensen *et al.*, 2014) for the different trophic groups.

The model selection procedure used by Ben Rais Lasram *et al.* (2020) allowed us to model distributions with at least two techniques for most species, with a few exceptions (i.e. climate model for *Pecten maximus*, *Sagartia troglodytes*, *Owenia fusiformis* and *Dicentrarchus labrax*; Habitat model for *Sagartia troglodytes* and *Raja clavata*). Furthermore, some species didn't have any retained habitat model (*Callionymus lyra*, *Chelidonichthys lucerna*, *Dicentrarchus labrax*, *Glycymeris glycymeris*, *Mullus surmuletus*, *Scyliorhinus canicula*, *Solea solea*, *Spondyllosoma cantharus*). Thus, when different selected models gave different predictions, it was necessary to consider this variability, and not only limit the choice to an average value. For each species, one random choice was made among the different predicted suitability index predictions for the climate model and habitat model, for where it exists. A total of 25 simulations were executed to consider the variability in the niche models predictions: this number was restricted due to i) the excess amount of time necessary to load time series and maps before running the scenarios, and

run the scenarios, and to ii) the space available to store the outputs. Before each of the 25 simulations, the new suitability indices were implemented for all concerned species.

We divided the 44 modelled species into 28 trophic groups of the EwE model (Table 1). Trophic groups in EwE could be composed by several species, and we used a weighted mean to create a trophic group map, *Map*, of suitability index per Ecospace grid cell for the different species, *s*:

$$Map_{trophic\ group} = \frac{\sum_s (Map_s \times Biomass_s)}{\sum_s Biomass_s} \quad (4)$$

Where the biomass is the simulation value obtained from SDMs in the scenario.

In the baseline scenario, the value was obtained from the Ecopath model. When we simulated a climate change scenario, the biomass was obtained by computing the change in the global suitability index created by the new scenario on the climate filter. This new suitability index could in theory become 0 in the entire Bay of Seine for some scenarios. Following Chaalali *et al.* (2016), the change between the sum of suitability index, *SuitInd*, in an RCP scenario, *scenario*, and in the current situation scenario, *current*, was considered as a change in biomass. We did this for each area, *area*, and species, *s*, constituting *Map_s*:

$$Biomass_{s,scenario} = Biomass_{s,current} \times \frac{\sum_{area} SuitInd_{s,area,scenario}}{\sum_{area} SuitInd_{s,area,current}} \quad (5)$$

The new biomass of the species was subsequently computed using its initial Ecopath biomass as base value. The new biomass of the trophic group was then obtained by summing the biomasses of the species composing it. For the species that we did not have niche models for, we assumed that they followed the same distribution as the rest of the group. To mimic the increase or decrease of the trophic group biomasses in Ecospace, we finally used this predicted biomass to force only the first year of time series in each simulation, letting the unconstrained biomasses evolve through the following years. The forcing of biomasses in Ecospace using Ecosim time series were done using the EwE version 6.6.15215.0.

In addition to biomass changes, we computed new habitat capacities for each trophic group concerned. In Ecospace the initial spatial distributions of trophic groups and vulnerable prey densities are driven by the habitat capacities, while search rates and potentially vulnerabilities are corrected according to their values (Christensen *et al.*, 2014). Habitat capacities are thus the strongest driver for trophic group distributions, along with trophic interactions.

The habitat capacity maps were changed according to the new parameters derived from each of the suitability index predictions. For each species represented by environmental preference maps, we chose to not drive them by other environmental or habitat parameters from the original model because all the main abiotic parameters are gathered within each environmental preference map, and thus weight the quality of the habitat for that species.

The simplified methodology of forcing species distributions in Ecospace is presented in the Figure 1.

Considering that the increase or decrease of trophic groups biomasses are predicted without trophic interactions in the niche models, and that the moving processes would be somehow progressive, a period of ‘spin-up’ had to be included in our simulation to consider the fact that some species could not reach or could exceed their abundance predictions with the trophic dynamics. After 25 years of spin-up, the evolution of the ecosystem was recorded for the next 50 years, the period that we speculate can reflect the state of the ecosystem under a particular climate scenario, to consider the large fluctuations of biomass that the trophic groups undergo.

2.5. Evaluation of climate scenarios with multiple indicators

To evaluate the impact of climate change on the Bay of Seine ecosystem, different indicators were observed at different levels. In order to observe only the impact, γ , of a climate scenario, *RCP*, on

the chosen indicators, *Indic*, and not their raw values, δ , relative impacts compared to the current climate scenario, *current*, were computed:

$$\gamma_{Indic_{RCP}} = \frac{\delta_{Indic_{RCP}} - \delta_{Indic_{current}}}{\delta_{Indic_{current}}} \quad (6)$$

On the trophic group scale, the average biomass, the standard deviation of the biomass and the fishing mortality per trophic group were evaluated. At the community scale, mean values of Mean Trophic Level (MTL; Pauly *et al.*, 1998), High Trophic level Indicator (HTI), representing the proportion of biomass of predators with a trophic level higher or equal to 4 (Bourdaud *et al.*, 2016), and total biomass were assessed. Finally, at fleet scale, the average volume, standard deviation of volume, average income per volume, and standard deviation of income per volume yielded were computed (the selling prices of the different groups are detailed in Table S9).

We hypothesized that the average biomass recorded during the last 50 years of simulations should be different from the initial value estimated from niche modelling, due to the effect of trophic interactions occurring in Ecospace. Comparisons of initial biomasses and simulated average biomasses were thus made to quantify the trophic interactions effect. This was accomplished by plotting relative initial and average biomasses on two axes: the first one on the x axis representing the value of the initial biomass, *I* (for Initial), of a trophic group with a climate scenario, *RCP*, relative to its initial value with the current situation, *current*: $(I_{i,RCP} - I_{i,current}) / I_{i,current}$, and the second one on the y axis representing the value of the average biomass *A* (for Average) of a trophic group with a climate scenario relatively to its initial value with the current situation: $(A_{i,RCP} - I_{i,current}) / I_{i,current}$.

This choice was oriented partly to avoid the overweighting of average biomasses compared to very low initial values, and to permit classifying the different groups into six discrete categories using ‘+’ and ‘-’ symbols, ‘--’ being negative and lower than ‘-’, itself lower than the positive

values ‘+’ and the maximum value ‘++’, in comparison to the initial biomass in the ‘current’ scenario (Table 2).

3. Results

Climate change predicted impacts were observed on two major levels, the biological component and the human exploitation component. Comparisons of the two RCP scenarios in this study, in terms of influence on these two major levels, are represented simultaneously, except where specified otherwise.

3.1. Biological impacts of the RCP scenarios

With the RCP2.6 conditions, 16 of the 40 trophic groups in EwE were predicted to suffer from a significant average biomass loss compared to the current climate scenario, while 12 were predicted to have a significant biomass increase, leaving 12 groups with minimal biomass changes (Figure 2). When simulating RCP8.5 conditions, the forecasted impact was more negative overall, with 20 groups having a significant biomass decrease, while 13 groups increased in biomass, leaving only 7 groups with minimal biomass changes. It is noteworthy that for the majority of trophic groups, the relative biomass with the RCP8.5 scenario represents an accentuated trend of the RCP2.6 evolution, either being negative or positive to the group.

When observing the forecasted variations around the average biomass with standard deviation values, only 5 and 6 different groups had significant reduced biomass variability in the RCP2.6 and RCP8.5 scenarios respectively, while 17 and 30 groups had a significant variability increase, leaving 18 and 4 groups within each scenario respectively with a comparable variability (Figure 3). Despite that more groups were predicted to have a significant biomass increase with the RCP8.5 scenario, the trends in biomass change compared to the current situation scenario were

similar to the average biomass trends observed from the RCP2.6 scenario. However, groups such as fish benthos feeders, sprat, poor cod and pouting showed a ten-fold variability increase between the current and RCP8.5 scenario.

All three community indicators demonstrated differences between scenarios. Stronger trends were observed in the RCP8.5 scenario than the RCP2.6 scenario. A decrease of the MTL was predicted in both RCP scenarios, however the predicted decrease of MTL was greater in the RCP8.5 scenario than in the RCP2.6 scenario: the highest decline of MTL predicted in RCP2.6 was around -2%, while predicted MTL decrease fell below this value in RCP8.5, especially in the Northwest with almost a -6% reduction (Figure 4a). In both RCP scenarios, a HTI decline was forecasted mostly in Northwest and Southeast, with predicted HTI decline around -25% in these areas in RCP2.6, and below -75% in these two areas in RCP8.5 (Figure 4b). Few changes in total biomass were predicted in RCP2.6 (mostly less than 5% increase), but biomass increased up to 15-20%, mostly in the Northern part of the Bay of Seine (Figure 4c). The indicators gathered here determined a global change in the Bay of Seine ecosystem towards a low trophic level-dominated situation following increasing warming conditions.

3.2. Fisheries impacts of the RCP scenarios

In the RCP2.6 scenario, three of the models predicted that fisheries would catch more in terms of income, two remained stable and dredge caught substantially less scallops (Table 3). In the RCP8.5 scenario, only the dredge was predicted to catch less than with the current climate in terms of income, while all other fleets caught more in most of the simulations, with rare losses for nets targeting demersals and crustaceans and pelagic trawls targeting demersals in some simulations. Additionally, fleets in RCP8.5 were predicted to catch more than in RCP2.6, except for nets targeting demersals and crustaceans.

The forecasting of income per volume was on average below the 5% change for five of the six fisheries modeled in the RCP2.6 scenario in comparison to the current situation, with only the bottom trawls targeting demersals and cephalopods slightly above 5% (Table 3). While in the RCP8.5 scenario, the latter was increased above 5% with 16% on average, while the ‘other fishing gears’ group also had an increase above the 5% threshold. The value is stable for dredge because they target only king scallop.

The income standard deviations on each simulation, representing the interannual variability of income for fishers, were predicted to increase on average between 50% and 100% for three of the fisheries modeled in the RCP2.6 scenarios, while it was decreased by 10% and 34% for Pelagic and bottom trawls targeting small pelagics and dredge respectively (Table 3). However, the variability among simulations was extremely high, and some income standard deviations were smaller in comparison to the baseline scenario in several simulations. In the RCP8.5 scenario, the forecasted fluctuations increased between 300% and 1000% for all the fisheries except dredge for which it was reduced by 79%, but the variability among simulations was smaller relatively to RCP2.6, and trends, positive or negative, were always uniform.

The predictions of income per volume yielded standard deviations, representing the interannual variability of income per volume yielded for fishers, were stable with the RCP2.6 and RCP8.5 scenarios for the Pelagic and bottom trawls targeting small pelagics (Table 3). In both scenarios, the stability of income per volume increased by 24% for the Pelagic trawls targeting demersals. For the three other fisheries, trends were different across the scenarios, with a high variability among simulations, but for the most part restrained on average between -25% and +25%.

In the RCP2.6 scenarios, the fishing mortality was predicted to be reduce for only 3 species, king scallop (-50%), plaice (-8%) and cod (-35%) (Figure 5), while it was predicted to increase up to 30% for nine groups, and >30% from the current situation for the nine remaining groups. In the

RCP8.5 scenario, only king scallop and cod fishing mortalities were reduced (-89% and -85% respectively), while fishing mortality was predicted to increase between 50% and 100% for five groups, and by >100% from the current situation for the fourteen remaining groups.

3.3. Added-value of trophic interactions

In the two forecasted scenarios, patterns of biomass comparison with initial values and final values were globally similarly proportionated across classes (Figure 6; Table S10). Observing only the direction of changes, RCP8.5 induced fewer deteriorating consequences, with more groups than RCP2.6 having I--A- and I+A- evolutions and more in I--A- and I-A+. No group in both scenarios had an A++A+ evolution, and only one group had an I+A++ evolution (i.e. poor cod in RCP2.6). However initial biomasses values for RCP8.5 were clearly predicted to be lower than in RCP2.6, where more groups reached a total decrease between 50% and 100% of their initial value in the current situation (Figure 6). Additionally, only one group in the RCP2.6 scenario had an average increase above 50% of the initial value for the current situation (i.e. bivalves filter feeders), while five groups in the RCP8.5 scenario had this increase (i.e. benthic invertebrates deposit feeders, bivalves filter feeders, fish benthos feeders, sprat and poor cod). Noticeably no error bar was represented on the x axis of the Figure 6 for readability, although some groups had large initial values fluctuations, which had consequences on the y axis results.

4. Discussion

4.1. Predicted impacts of climate change on the Bay of Seine

Our results demonstrated clear impacts of climate change in both scenarios (i.e. RCP2.6 and RCP8.5), however, there were noticeably stronger trends in the case of RCP8.5 evolution. At the biological level, these results emphasize the fact that effects of climate change are not uniform

across trophic groups, e.g., with some stocks collapsing, such as plaice, gurnard and cod, others concurrently remaining stable compared to the current situation, such as flounder or planktivorous fish, and some even expanding on average in the RCP8.5 scenario, such as bivalves filter feeders, sprat or poor cod. These results are in line with Fulton (2011), arguing that there will be ‘winners and losers’ with climate change. This holds true for both large and small scale changes, and is ecosystem-specific. The Bay of Seine is part of the North Atlantic, an area subject to strong shifts under climate change (Burrows *et al.*, 2019). The predicted biomass distribution created among both scenarios is evolving towards an ecosystem dominated by low trophic level species, probably favored by the decrease of predation pressure, one of the processes implied in the trophic amplification (Lotze *et al.*, 2019). This evolution is comparable to the concept of ‘fishing down the marine food web’ resulting from high fishing pressure oriented on high trophic levels (Pauly *et al.*, 1998; Gascuel, 2005). The Bay of Seine ecosystem reacts to climate change as one under high fishing pressure resulting in a modification of its structure.

In addition to the average value of stocks biomasses, our results also focused on the variability of the group biomasses, and showed that they had markedly increased, especially in the RCP8.5 scenario, illustrated by periodically alternating phases of high abundances with others of relatively low abundances. This raise of variability was predicted for the groups with an increased average biomass, but also for some undergoing a decline, like mackerel, benthopelagic cephalopods, or pilchard. One of the reasons that can be attributed for this rise is the predicted decline of almost all top fish and cephalopods trophic levels (i.e. fish piscivorous, whiting, cod, sharks, rays, seabass and benthopelagics cephalopods, see Figure 2). Indeed, top predators are known to favor the stability of ecosystems by maintaining low prey densities and fluctuations (Bax, 1998; Hollowed *et al.*, 2000; Mangel and Levin, 2005; Wilmers *et al.*, 2007; Kirby *et al.*, 2009). At the local Eastern English Channel scale, several studies already emphasized the important control of cod

and whiting, here depleted, on the lower trophic levels using different modelling approaches (Girardin *et al.*, 2016; Travers-Trolet *et al.*, 2020). Gadoids, especially, are known to be negatively affected by warming (Free *et al.*, 2019), thus, such an event is predictable. Ecological Networks Analysis (ENA; Ulanowicz, 1986; Saint-Béat *et al.*, 2015; Lau *et al.*, 2017) could not be represented at the time of the Ecospace simulation in this study, but it could bring a new vision of the functional and structural properties of the ecosystem beyond classical community indicators (Safi *et al.*, 2019), and will be explored in a forthcoming article (Araignous *et al.*, in prep.).

These forecasts must be interpreted in terms of trends of evolution, as several phenomena could not be included in these simulations. This was part of the reason why the results were demonstrated in terms of relative impact and not absolute values. The initial parameterization lacked the effect of the different RCP scenarios on several compartments of the ecosystem, especially for the lower trophic levels (e.g. phytoplankton and zooplankton) and apex predators (i.e. birds and marine mammals), which could have non-negligible bottom-up and top-down effects respectively, in addition to their identity as climate and ecosystem sentinels (Hazen *et al.*, 2019). The former were not represented in this study due to the lack of available predicting models when the development of the methodology was realized, although some do exist and have been used for predictions in other studies that showed that they could have impacts on the whole trophic cascade (e.g. Brown *et al.*, 2010; Araújo and Bundy, 2012; Guo *et al.*, 2019). Concerning apex predators, their homoeothermic metabolism, high mobility and dependence on prey availability make their distribution difficult to predict (Crick, 2004; Simmonds and Isaac, 2007). However, a broad scale of trophic levels was represented in our simulations and permitted observation of several mechanisms involved in the ecosystem's possible evolutions. Additionally, Ecospace modelling is mainly based on a fitted Ecosim model (plus some extra parameters, e.g. base dispersal rate or the maps), itself being based on an Ecopath model representing an equilibrium

state of an ecosystem during a precise period. Unfortunately, this representation does not consider the species that are not in the area but could arrive due to changing conditions, and can potentially deteriorate ecosystems (Occhipinti-Ambrogi, 2007). Empirical evidences demonstrated large movements of indigenous and non-indigenous species in the area: an abrupt northward shift of small pelagics from the Eastern English Channel to the North Sea occurred in the middle of the 1990's, partly due to climate conditions (McLean *et al.*, 2018), while for the first time Mediterranean species were recently recorded in the Eastern English Channel (Mahé *et al.*, 2012; 2014), and a tropical species was recorded in the North Sea (Cresson *et al.*, 2017). In general, stocks with smaller body size and faster life history characteristics will better adapt to warming (Perry *et al.*, 2005; Free *et al.*, 2019; Moullec *et al.*, 2019). One approach to assess this, similar to the work done with Ecosim on invasive species by Langseth *et al.* (2012), can be used, but this would require new parameterization for such species and several assumptions concerning their foraging relationships with other trophic groups already present in the area, a main modelling challenge for future scenarios of global change (Corrales *et al.*, 2020).

Effects of climate change were also predicted on fisheries, focusing on income and income per yielded volume obtained by fishers in the two RCP scenarios. Our results indicated surprisingly that most of the fisheries would see their average earned value increase, and even doubled for bottom trawlers targeting demersals and cephalopods in the RCP8.5 scenario, confirming assumptions that some fisheries could be advantaged by indirect effects of climate change (e.g. Ainsworth *et al.*, 2011). This is in contradiction with global fisheries projections, which are expected to decrease (Lam *et al.*, 2016). However, conclusions about these results must be dampened for different reasons. First, our simulations are based on a constant price hypothesis, while fish price is actually known to evolve according to different parameters including offer and other species' prices (Loannides and Whitmarsh, 1987). It is thus probable that a high availability

of certain stock would induce a decrease in their income per kg, hindering such fungibility (i.e. replacing one entity by another of equal utility) for fishers. Secondly, the income per volume demonstrated in our results, contrary to expectations, showed that fishers for the majority do not fish more volume to earn the estimated income, and even have a positive income per volume index increase between 5% and 25% on average for bottom trawls targeting demersals and cephalopods. However, a major impediment is the stability of the revenue fishers can earn, which, according to our results, is predicted to be extremely low, at least in RCP8.5, and in a main part of RCP2.6 simulations, despite being highly unpredictable. Fishers' revenue stability is known to be one of the most important drivers for fishing activity, above potential high revenue for most fisheries (Holland, 2008; de Vos *et al.*, 2016). Indeed, it is obvious that without permanent acceptable revenue, fishers are not able to pay the common variable and fixed costs, including the payment of crew's salary or vessel maintenance. Moreover, our observed results considered no limiting quotas, although quota limits would have consequences on the ability of fishers to target some commercial species, especially in a landing obligation context (European Commission, 2013; Borges, 2015), and thus decline fishers' profit. Future studies should associate fisheries management target scenarios with climate ones (Gaines *et al.*, 2018; Barange, 2019), as done by Bauer *et al.* (2019) who, using Ecospace, highlighted simulations the importance of different management strategies on biodiversity and catch value. These models could also test different scenarios of quota allocations which should evolve with changes of fish distributions (Baudron *et al.*, 2020).

When observing the results per fishery, it is noticeable that dredgers, only targeting king scallop, are the only fleet to observe a clear decline of profit, while their target species is expanding. This result must be examined carefully because it arises from an eastward shift in the distribution of king scallop, creating an invulnerable portion of the stock due to the inaccessibility of dredgers in

that eastward region. Indeed, dredgers activity is restricted to a certain area in the original model, corresponding to the preferential habitat area for king scallop, but this changed throughout scenarios. Hence the fishing mortality of king scallop, along with cod are the only two to decrease in the RCP scenarios compared to the current situation. Likewise, king scallop exploitation is highly restricted and controlled (Carpentier *et al.*, 2009). However, the different small-scale restrictions could not be clearly represented in the current Ecospace model. Thus, our predictions concerning scallop must be tempered for this reason.

Concerning cod, the most probable explanation is that the decreased stock abundance makes it an uninteresting target for fishers who prefer focusing their effort on other more abundant stocks. This re-focus of effort is keeping the fishing mortality high on the other groups, which, in part, prevents them from expanding: this is one of the main parameters inducing changes between niche modelling predicted abundances with trophic and fisheries interactions. Such fishers' reaction against cod is plausible, as more diversified fisheries are an insurance of better resilience to perturbations such as climate change (Lagarde *et al.*, 2017; Yletyinen *et al.*, 2018).

4.2. Added-value of trophic interactions on climate forecasting

One of the major improvements of this study is to provide an extension from the 'Fundamental niche' to the 'realized niche' prediction of ecosystem biomass distributions, an important feature of species distributions (Lany *et al.*, 2018). Hinging on the framework proposed by Chaalali *et al.* (2016), this study extended the analysis using EwE trophodynamic equations to bring new insights. According to our results, the effects of trophic interactions in the Bay of Seine seem to be balanced, with more positive than negative effects, coinciding with the conclusions of Bates *et al.* (2017). However, this trend can be divided in two parts having a completely different evolution: the groups with a niche modelling and those without. The groups without niche

modelling were not constrained in their initial values, thus their average biomass only changed through the trophic interactions, which differed within scenarios. Here, this comparison emphasized a decline for birds and marine mammals, presumably due to the decline of their prey. For the groups that had a different initial abundance with niche modelling, the results are more oriented towards positive effects. If a few species undergo a decline, most of the groups increase in comparison to their initial value from niche modelling, with some even outweighing the average value observed in the current situation scenario. In the RCP8.5 scenario, most groups start with a lower biomass than in the RCP2.6 scenario, and are more capable of increasing, with the help of the vulnerability settings implemented in EwE (Christensen *et al.*, 2008). In this context, the vulnerability parameter value given to poor cod was arbitrarily set to default (2) and a better way to estimate it could be a future improvement, for example through longer time series or manual fitting from Ecospace outputs.

Some results regarding the ability of some groups to increase in abundance while having a low initial biomass value associated with adverse environmental conditions were surprising. It must be considered that one of the limitations of our methods was the inability to vary the vital rates of trophic groups which can prevent them from developing: such was evoked by Serpetti *et al.* (2017) and Bentley *et al.* (2017) for Ecosim, even without fisheries or beneficial trophic conditions. Such environmental conditions can be directly detrimental for survival, especially in early life stages (e.g. Baumann *et al.*, 2012; Frommel *et al.*, 2012; Boch *et al.*, 2018; Sguotti *et al.*, 2019). It can also indirectly induce a decrease of predation potential, as seen in sharks by Pistevos *et al.* (2015), as well as influence the size of individuals in a population (Queirós *et al.*, 2018; Catalán *et al.*, 2019), a fundamental parameter of fish trophic interactions (Scharf *et al.*, 2000; Shin and Cury, 2001). Finally, ocean acidification and oxygen depletion, which could have impacts on a variety of species (Breitburg *et al.*, 2018; Olsen *et al.*, 2018), are also not represented in our models.

Some groups under the RCP8.5 scenario reached high abundance levels, particularly sprat and poor cod, which are species not caught by fishers. Such observations highlight the important consideration that the evolution of species under climate change situation won't only be influenced by environmental change and trophic interactions, but also by fishing operations. The production surplus for sprat and poor cod is not taken by fisheries, while other species undergo a high fishing mortality due to unrestricted effort and target change. This major role of fisheries in climate change effect has already been highlighted by several authors (e.g. Planque *et al.*, 2010; Sumaila and Tai., 2019; Woodworth-Jefcoats *et al.*, 2019).

4.3. Towards reliable predictions of climate scenarios

The uncertainties regarding the evolution of ecosystems with climate change are numerous (Bryndum-Buchholz *et al.*, 2019; Lotze *et al.*, 2018). In this study, the model forecasts were evaluated using 25 simulations, in order to obtain an overview of the uncertainty of the results according to the niche models used, with uncertainty being a tremendous feature of climate projections (Payne *et al.*, 2016). The results demonstrated limited uncertainty in our results, highlighting converging trends in the RCP2.6 and RCP8.5 scenarios compared to the current situation scenario and between themselves.

However, areas of uncertainty in the model are still present, beginning with the quality of input parameters used in the model, which could be further explored (Christensen and Walters, 2004; Lassalle *et al.*, 2014). In Ecospace, fisheries are driven by a gravity model, giving fishers the requirement to fish according to their feasibility in proportion to the 'money in the sea'. In reality, the drivers involved in fishers' behavior are numerous (van Putten *et al.*, 2012; Girardin *et al.*, 2017). In our simulations, the fishing mortalities undergone by commercial species were calculated on a fixed effort for fisheries, without management pressures. Though, it is obvious

that the targeting of commercial species will be reduced due to reduced quota availability, which reflects the decline of Spawning Stock Biomass. This is especially noticeable for classical target species such as sole, cod or whiting whose conservative productivity will be focused on. Future simulations should consider fisheries management and its interaction with fish availability to simulate more realistic biomass evolutions.

Fish availability for fishing is dependent both on the fish and the fishers' ability to distribute freely in the area: the impacts of these cumulative effects has to be explored (Fu *et al.*, 2019; Hodgson *et al.*, 2019). In the Bay of Seine, multiple activities apart from fishing currently occur and will occur in the forthcoming years, including OWF (Raoux *et al.* 2017; 2019), dumping of dredged material (Pezy *et al.*, 2017), aggregate extraction and all other types of maritime traffic other than fishing (Marchal *et al.*, 2014a; 2014b). Their impact on fish and fisheries in the Eastern English Channel has been partially observed or simulated (Marchal *et al.*, 2014a, 2014b; Girardin *et al.*, 2015; Tidd *et al.*, 2015), and future forecasts that are already in progress will involve the integration of these multiple activities to observe synergetic or antagonistic potential effects (Noguès *et al.*, in prep.).

Our simulations considered the state of the ecosystem in 2100 to derive ecological or fisheries indicators. However, it is important to remember that events occurring in the ecosystem with different climate trajectories will be influenced by their timing, meaning that some species' environmental preferences will make them move faster than others. That is why we must keep in mind that running all the species together with niche modelling forcing is likely to differ from running an evolving environment with a 2000-2100 time series. Some of latest improvements of Ecospace (Steenbeek, 2012; Steenbeek *et al.*, 2013), not used in this study, have the potential to lead such simulations, and this approach should be further analyzed in the forthcoming years.

5. Conclusion

In this study, niche models with multiple climate scenarios were used as forcing parameters for a spatially-explicit trophic Ecospace model developed in order to observe the impact of different climate change trends on the French Bay of Seine. The simulations predicted that both the RCP2.6 and RCP8.5 scenarios will have repercussions for the Bay of Seine ecosystem and the fisheries exploiting them, with stronger divergences for the RCP8.5 scenario. In general, the stronger the radiation is, the stronger the instability of the ecosystem could be. In addition, we emphasized that some species would increase partly due to trophic reorganizing (see Figure 6, Table S10), and that fishing pressure is a major parameter of the evolution of species abundance under different climate change scenarios. By forcing niche models in a trophic interactions model, the importance of the latter was highlighted in a way to support plausible predictions. At the broader scale of climate change forecasting, models like Atlantis (Fulton *et al.*, 2007) can offer a larger spectrum of scales and a multimodel, multiple scale approach must be promoted (Peck *et al.*, 2016; Bryndum-Buchholz *et al.*, 2019): this is the only way to identify key parameters shaping the potential future of marine ecosystems.

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Data Availability Statement

Data available on request due to privacy/ethical restrictions.

Conflict of interest

None of the co-authors has any potential conflict of interest.

Author contribution

Pierre Bourdaud: development of the study methodology, running and exploitation of the simulations, writing of the manuscript.

Frida Ben Rais Lasram: development of the niche models, development of the study methodology.

Emma Araignous: development of the study methodology, discussions on Ecospace.

Juliette Champagnat: development of the study methodology, discussions on Ecospace.

Samantha Grusd: correction of English in the manuscript, discussions on Ecospace.

Ghassen Halouani: development of the original Ecopath, Ecosim and Ecospace models, development of the study methodology, discussions on Ecospace.

Tarek Hattab: development of the niche models.

Boris Leroy: development of the niche models, development of the study methodology.

Quentin Noguès: development of the study methodology, discussions on Ecospace.

Aurore Raoux: development of the original Ecopath model.

George Safi: development of the study methodology.

Nathalie Niquil: development of the original Ecopath model, development of the study methodology.

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Figures and tables legends

Figure 1: Flow diagram of the methodology used in the study to force species distributions in Ecospace. SDMs: species distribution models, noted m from 1 to 9 for each of the predictive responses (see Ben Rais Lasram *et al.*, 2020). s : species, from 1 to k , the total number of species available through SDMs.

Figure 2: Relative average biomass changes in the RCP2.6 and RCP8.5 scenarios in comparison to the current situation scenario.

Figure 3: Relative biomass standard deviation changes in the RCP2.6 and RCP8.5 scenarios in comparison to the current situation scenario.

Figure 4: Average relative A) Mean Trophic Level (MTL), B) High Trophic level Indicator (HTI) and C) Total Biomass (TB) changes in the RCP2.6 (left) and RCP8.5 (right) scenarios in comparison to the current situation scenario.

Figure 5: Relative fishing mortality changes in the RCP2.6 and RCP8.5 scenarios in comparison to the current situation scenario.

Figure 6: Comparison, for each trophic group, of the final relative average biomasses (A) and the initial relative biomass (I) compared to the initial values with the baseline situation scenario in the scenarios RCP2.6 (top) and RCP8.5 (bottom).

Table 1: Species with climate model per trophic groups in the Ecopath model, and the presence of a habitat model. * indicates species with no retained habitat model. See Ben Rais Lasram *et al.* (2020) for further details concerning model selection.

Table 2: Categories, codes and global impact for trophic groups in the assessment of the effect of trophic interactions on biomasses in climate scenarios. “+” indicates an increase compared to the initial biomass value, “-” a decrease, while with similar Average biomass for a RCP scenario

(A_{RCP}) and Initial biomass for the same RCP scenario (I_{RCP}), the signs “++” or “--” indicate the highest or lowest value, respectively.

Table 3: Average number of groups in each of the biomass evolution classes compared to the initial values in the current situation scenario. $\pm$ values represent the standard deviations of the number of groups for each indicator among replicates.

Figures

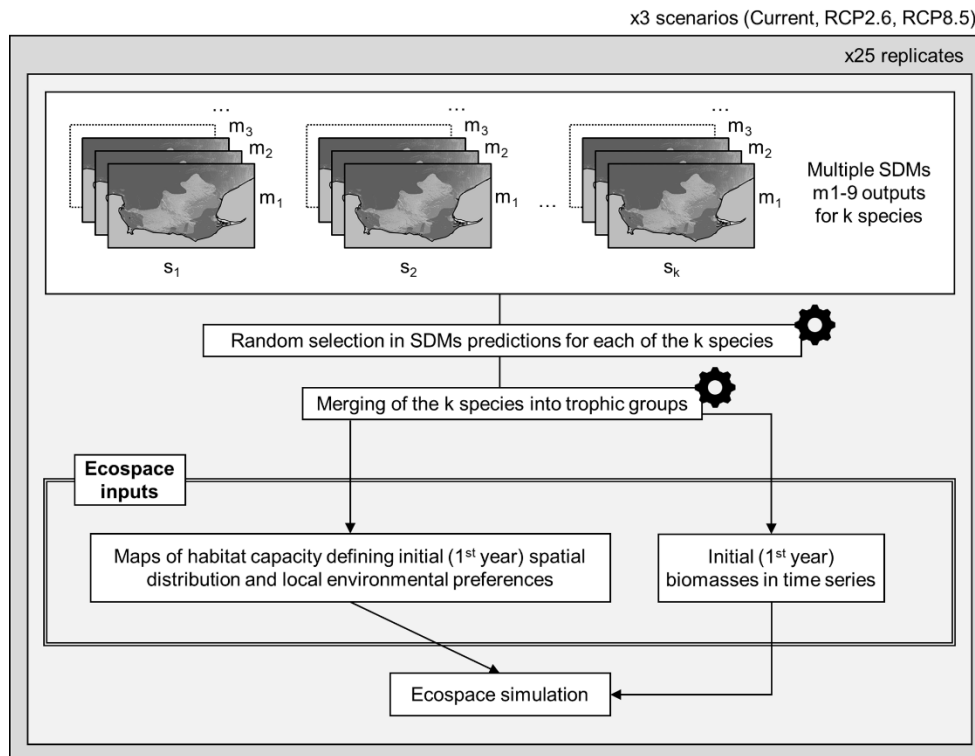


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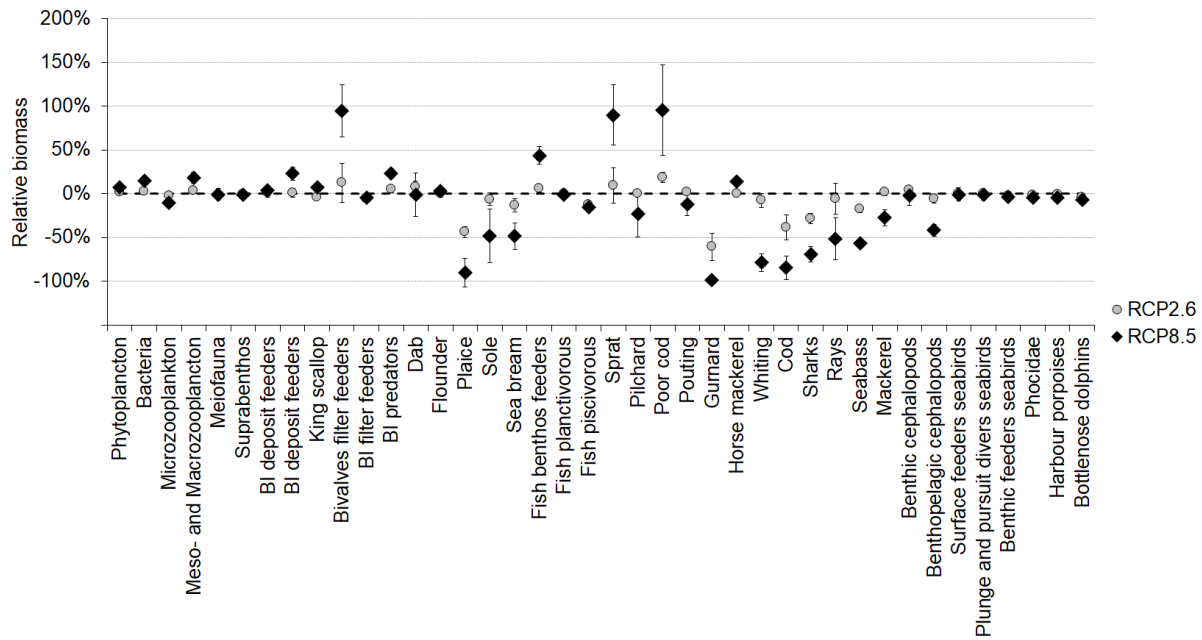


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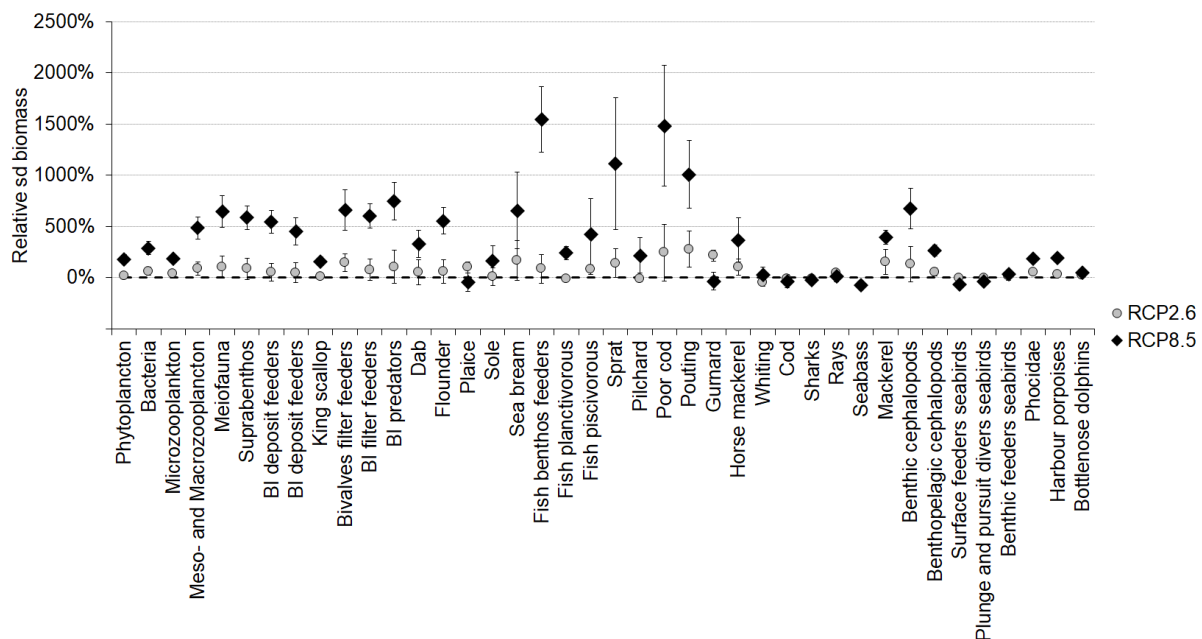


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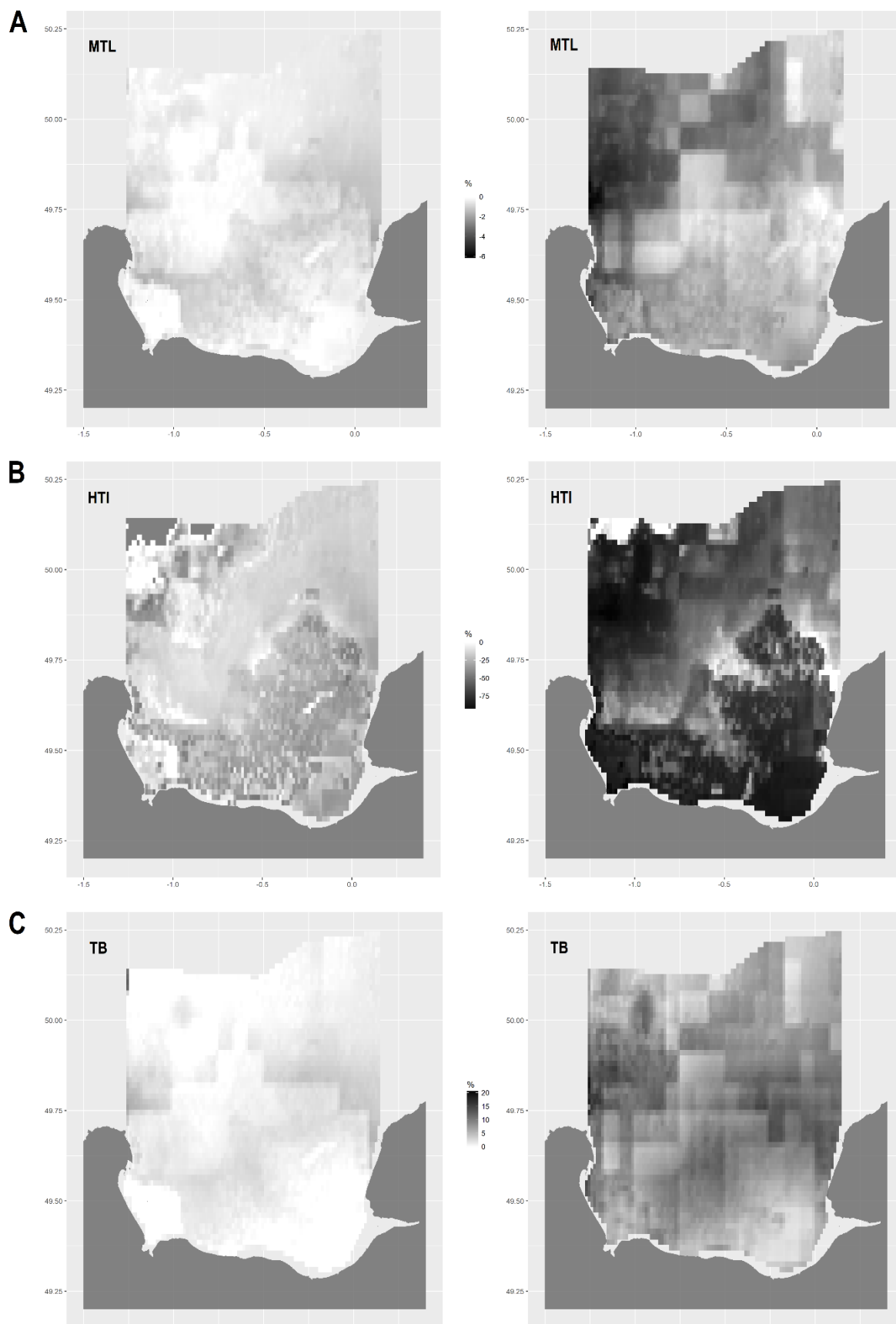


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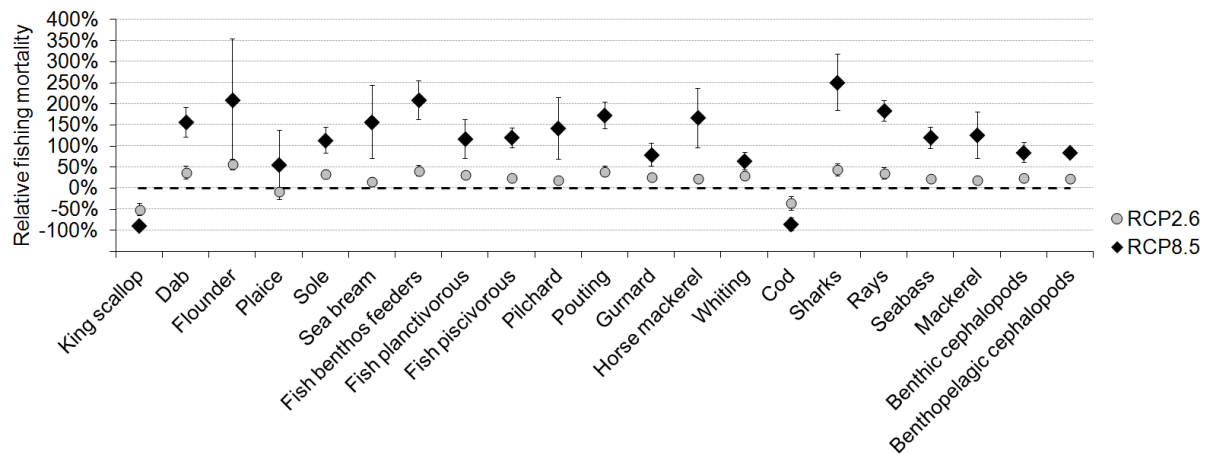


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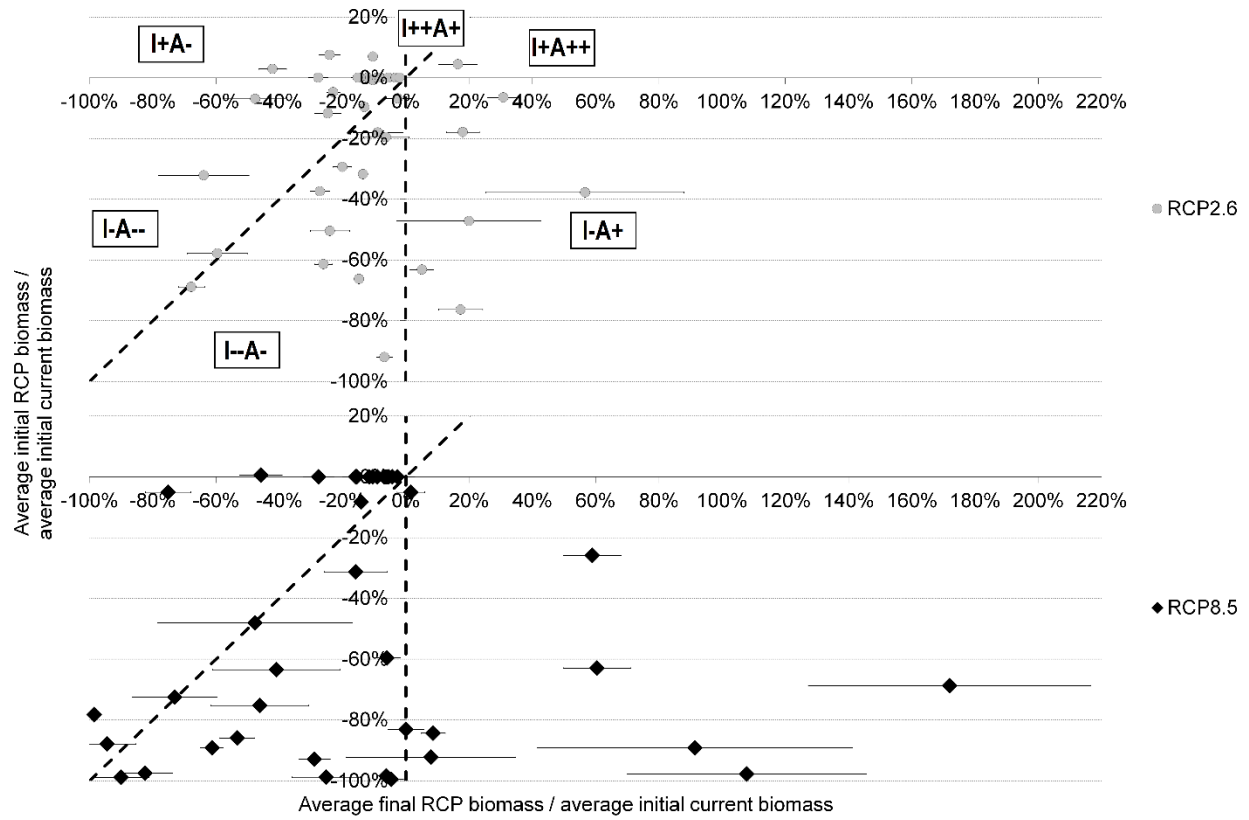


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Tables

Table 1: Species with climate model per trophic groups in the Ecopath model, and the presence of a habitat model. * indicates species with no retained habitat model. See Ben Rais Lasram *et al.* (2020) for further details concerning model selection.

Ecopath trophic group	Latin name	Habitat model
Bivalves filter feeders	<i>Aequipecten opercularis</i>	X
	<i>Ensis directus</i>	X
	<i>Glycymeris glycymeris</i>	X*
	<i>Lanice conchilega</i>	X
Benthic invertebrates deposit feeders (Subsurface)	<i>Echinocardium cordatum</i>	X
Benthic invertebrates deposit feeders (Surface)	<i>Ophiothrix fragilis</i>	X
	<i>Pectinaria koreni</i>	X
King scallop	<i>Pecten maximus</i>	X
Benthic invertebrates filter feeders	<i>Psammechinus miliaris</i>	X
Benthic invertebrates predators	<i>Asterias rubens</i>	X
	<i>Buccinum undatum</i>	X
	<i>Owenia fusiformis</i>	X
	<i>Sagartia troglodytes</i>	X
Benthic cephalopods	<i>Sepia officinalis</i>	X
Benthopelagic cephalopods	<i>Alloteuthis subulata</i>	
	<i>Loligo vulgaris</i>	
Dab	<i>Limanda limanda</i>	X
Flounder	<i>Platichthys flesus</i>	X
Plaice	<i>Pleuronectes platessa</i>	X
Sole	<i>Solea solea</i>	X*
Sea bream	<i>Spondyllosoma cantharus</i>	X*
Fish benthos feeders	<i>Callionymus lyra</i>	X*
	<i>Mullus surmuletus</i>	X*
	<i>Labrus bergylta</i>	X
	<i>Zeus faber</i>	
Fish planktivorous	<i>Clupea harengus</i>	
	<i>Engraulis encrasicolus</i>	
Fish piscivorous	<i>Pollachius pollachius</i>	
Sprat	<i>Sprattus sprattus</i>	
Pilchard	<i>Sardina pilchardus</i>	
Poor cod	<i>Trisopterus minutus</i>	
Pouting	<i>Trisopterus luscus</i>	
Gurnard	<i>Chelidonichthys lucerna</i>	X*
	<i>Chelidonichthys lastoviza</i>	X
Horse mackerel	<i>Trachurus trachurus</i>	

Whiting	<i>Merlangius merlangus</i>	
Cod	<i>Gadus morhua</i>	
Sharks	<i>Mustelus mustelus</i>	X
	<i>Scyliorhinus canicula</i>	X*
	<i>Scyliorhinus stellaris</i>	X
Rays	<i>Raja clavata</i>	X
	<i>Raja montagui</i>	X
Seabass	<i>Dicentrarchus labrax</i>	X*
Mackerel	<i>Scomber scombrus</i>	

Table 2: Categories, codes and global impact for trophic groups in the assessment of the effect of trophic interactions on biomasses in climate scenarios. “+” indicates an increase compared to the initial biomass value, “-” a decrease, while with similar Average biomass for a RCP scenario (A_{RCP}) and Initial biomass for the same RCP scenario (I_{RCP}), the signs “++” or “--” indicate the highest or lowest value, respectively.

Category	Code	Impact
$A_{RCP} < I_{RCP} < I_{current}$	I-A--	Negative
$I_{RCP} < A_{RCP} < I_{current}$	I--A-	Positive
$I_{RCP} < I_{current} < A_{RCP}$	I-A+	Positive
$I_{current} \leq I_{RCP} < A_{RCP}$	I+A++	Positive
$I_{current} < A_{RCP} < I_{RCP}$	I++A+	Negative
$A_{RCP} < I_{current} \leq I_{RCP}$	I+A-	Negative

Table 3: Average number of groups in each of the biomass evolution classes compared to the initial values in the current situation scenario. $\pm$ values represent the standard deviations of the number of groups for each indicator among replicates.

Fishery	RCP	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagics	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
Relative average	RCP2.6	24 $\pm$ 9	4 $\pm$ 6	25 $\pm$ 7	1 $\pm$ 7	14 $\pm$ 3	-53 $\pm$ 14

income (%)	RCP8.5	7 ± 13	49 ± 18	97 ± 19	42 ± 44	27 ± 6	-92 ± 2
Relative average income per volume (%)	RCP2.6	5 ± 3	$< 1 \pm < 1$	7 ± 2	-2 ± 1	5 ± 1	0 ± 0
	RCP8.5	-1 ± 11	$> -1 \pm < 1$	16 ± 9	-3 ± 3	8 ± 2	0 ± 0
Relative income standard deviation (%)	RCP2.6	58 ± 114	-10 ± 15	86 ± 119	38 ± 51	98 ± 164	-34 ± 25
	RCP8.5	373 ± 124	396 ± 163	957 ± 195	614 ± 134	633 ± 141	-79 ± 4
Relative income per volume standard deviation (%)	RCP2.6	-7 ± 15	$< 1 \pm < 1$	-11 ± 26	-24 ± 5	-4 ± 17	0 ± 0
	RCP8.5	3 ± 10	$> -1 \pm < 1$	16 ± 9	-24 ± 3	14 ± 2	0 ± 0