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Abstract

The consequences of climate change for marine organisms are now well-known, and include metabolism and behavior modification, distribution area shifts and changes in the community. In the Bay of Biscay, the potential environmental niches of subtropical non-indigenous species (NIS) are projected to expand as a response to sea temperature rise by the mid-century under the RCP8.5 climate change scenario. In this context, this study aims to project the combined effects of changes in indigenous species distribution and metabolism and NIS arrivals on the functioning of the Bay of Biscay trophic network. To do this, we created six different Ecopath food web models: a "current situation" trophic model (2007–2016) and five "future" trophic models. The latter five models included various NIS biomass combinations to reflect different potential scenarios of NIS arrivals. For each model, eight Ecological Network Analysis (ENA) indices were calculated, describing the properties of the food web resulting from the sum of interactions between organisms. Our results illustrate that rising temperature increases the quantity of energy passing through the system due to increased productivity. A decrease in the biomass of some trophic groups due to the reduction of their potential environmental niches also leads to changes in the structure of the trophic network. The arrival of NIS is projected to change the fate of organic matter within the ecosystem, with higher cycling, relative ascendency, and a chain-like food web. It could also cause new trophic interactions that could lead to competition and thus modify the food-web structure, with lower omnivory and higher detritivory. The combined impacts (increasing temperatures and NIS arrivals) could lower the resilience and resistance of the system.

Key words: climate change, non-indigenous species, Ecological Network Analysis, food web modeling, fisheries

1. Introduction

The impacts of climate change on marine biodiversity and ecosystem functioning have been extensively studied over the last two decades (Harvell et al., 2002; Poloczanska et al., 2013; Lenoir et al., 2020). At the global scale, several studies have predicted the effects of climate change on marine ecosystems (Parmesan and Yohe, 2003; Butchart et al., 2010; Poloczanska et al., 2013; Lotze et al., 2019), but there remains a need for local studies that take into account environmental drivers in order to adapt management policies (Lopez y Royo et al., 2009; Riera et al., 2016), especially in coastal areas already subject to different human-induced pressures (eutrophication, fishing, recreational activities, pollution, marine structures such as windfarms, etc.). Furthermore, climate change is expected to have greater impacts on coastal areas than on the open ocean (Wong et al., 2014). As a consequence of rising temperatures and the arrival of subtropical species (Cheung et al., 2012), marine communities in temperate coastal areas are increasingly subject to tropicalization (Vergés et al., 2014; Montero-Serra et al., 2015).

The Bay of Biscay is located in the northeastern part of the Atlantic Ocean, along the west coast of France, in temperate latitudes already affected by warming temperatures (Michel et al., 2009; Irigoien et al., 2011; Costoya et al., 2015). This temperature change has induced a modification in local fish communities, with decreasing abundance and a shift in distribution range (Costoya et al., 2015; Iglésias and Lorance, 2016; Delgado et al., 2018). Indeed, a recent study projecting the potential environmental niches of 163 indigenous species revealed that some of these species would shift westward or northward by 2050 under scenarios RCP2.6 and RCP8.5 (Le Marchand et al., 2020). This study also projected the arrival of southern non-indigenous species (NIS) in the Bay of Biscay as a consequence of a northward shift of their native ranges. A major limitation of this study, however, was that it did not consider trophic interactions. Indeed, trophic interactions among species create a complex network of fluxes, as a result of organism feeding suitability, such as in terms of predation or herbivory (Montoya et al., 2006). There is now evidence that warming temperatures affect ecosystem trophic dynamics (Lercari et al., 2018; Kwiatkowski et al., 2019; Baird et al., 2019), notably due to the effects of trophic cascades (Doney et al., 2012). Furthermore, it has been proven that the arrival of invasive species may alter the structure and functioning of food webs (Baxter et al., 2004; Nehls et al., 2006; Baird et al., 2012). However, to our knowledge, there are very few studies on the consequences for a local trophic network of the arrival of NIS due to a shift of their distribution area under climate change, in a temperate ecosystem (Moullec et al., 2019a).

In the Bay of Biscay, Le Marchand et al. (2020) revealed that under the RCP8.5 scenario, 54% of fish and cephalopod species would not undergo any range shift by 2050. . These authors defined NIS as species currently beyond the southern border of the Bay of Biscay and whose area of presence is projected to expand with climate change. These are not invasive species *sensu stricto* (i.e., introduced by humans, having no predators,

opportunistic, and capable of rapid and dramatic increases in abundance; Mack et al., 2000). In the context of climate change, little work has been done on the combined impacts of changes on (1) indigenous species distribution and metabolism, and (2) NIS arrivals affecting trophic network properties. These aspects are, nevertheless, crucial for ecosystem management and policies (Halpern et al., 2015).

Given the impacts of climate change on the structure and functioning of marine ecosystems, it is necessary to have reliable indicators that make it possible to follow and anticipate ecosystem changes. Several types of indicators, such as Ecological Network Analysis (ENA) indices, describe ecosystem functioning. Ecological network analysis provides a set of indicators based on the analysis of the quantified flux (carbon or energy) within a trophic network (Ulanowicz, 1986; Niquil et al., 2012). The main goal of these indicators is to characterize the functioning of a system (Niquil et al., 1999) and to emphasize the holistic properties of the food web (Fath et al., 2007). They make it possible to assess how the trophic network may be modified following different changes in the ecosystem (Baird et al., 1991). For instance, ENA indices can be used to explore how a system will evolve following environmental change (Paar et al., 2019) or anthropogenic pressure (Bueno-Pardo et al., 2018). In recent years, ENA indices have been proposed as highly promising indicators for assessing the "Good Environmental Status" of marine ecosystems (Niquil et al., 2012), targeted by the “Food Webs” descriptor of the Marine Strategy Framework Directive (Safi et al., 2019; Fath et al., 2019) and proposed as tools for environmental managers (Schukel et al., 2018).

The aim of the present study was to investigate the possible consequences of climate change by coupling effects on indigenous species, consisting in a potential decrease in their environmental niches and modifications to their metabolism, with the arrival of NIS in the same area. The trophic functioning of the Bay of Biscay ecosystem was assessed by applying various biological hypotheses for the mid-century and the RCP8.5 climate change scenario. To do this, Ecopath models and ENA indicators were applied to the Bay of Biscay. To consider the potential future NIS biomass, six models were built that progressively varied the NIS biomass.

2. Material and methods

2.1. Study area

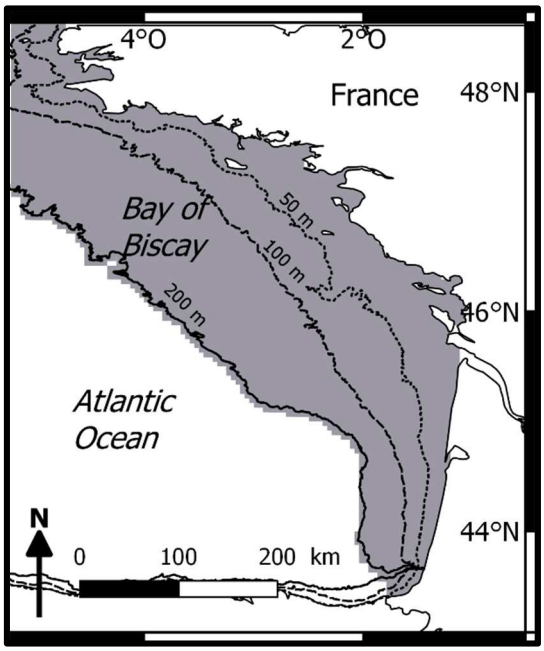

Figure 1: Geographical location of the study area: in grey, the French part of the Bay of Biscay continental shelf (30–200 meters depth)

The Bay of Biscay is a large gulf located on the Eastern side of the North Atlantic Ocean (Figure 1). It is bordered by the Spanish (43.5°N) and French coasts and by the English Channel and the Celtic Sea to the north (48.3°N). It is the top fishing area in Europe (ICES, 2020), with about 100,000 tonnes of fish and shellfish caught every year by French and other European fishermen (http://ices.dk/marine-data). Our study focused on the French part of the Bay of Biscay continental shelf (30–200 m depth). The Bay of Biscay is already affected by climate change, with its sea temperature in the upper 200 m layer increasing by 0.2°C.decade^{-1} between 1965 and 2004 (Michel et al., 2009) and general trends of changes in temperature seasonality have already been observed (Costoya et al., 2015). In addition, Chust et al. (2021) reported an increase in chlorophyll concentrations measured by satellite of 0.054±0.012 mg m^{-3} dec^{-1} in the Bay of Biscay during the last two decades.

2.2. Ecopath model

The Ecopath with Ecosim (EwE) model is a tool used worldwide for modeling marine trophic networks. In this study, the 6.6 version of Ecopath was used. The Ecopath routine provides a snapshot of energy fluxes between different functional groups, from plankton to marine mammals (Christensen and Walters, 2004). A functional group is composed of one to several species with identical trophic behavior.

With Ecopath, the energy fluxes are modeled using two main equations. The first equation calculates production. It corresponds to the sum of all the outgoing fluxes and is defined as:

Production = fishery catch + predation mortality + net migration + biomass accumulation + other mortalities

Formally, for a functional group *i* and a predator *j* (*j* being a predator of *i*), this equation can be written as:

$$B_i \times (P/B)_i = Y_i + \sum_j (B_j \times (Q/B)_j \times DC_{ij}) + Ex_i + Bacc_i + B_i(1 - EE_i) \times (P/B)_I \quad (1)$$

where B is the biomass density ($t.km^{-2}$), P/B is the production rate ($year^{-1}$), Y is the total catch ($t.km^{-2}$), Q/B is the consumption rate ($year^{-1}$), DC is the diet composition (DC_{ij} is the proportion of *i* in the diet of *j*), Ex is the net migration rate ($year^{-1}$), Bacc is the biomass accumulation ($year^{-1}$), and EE is the ecotrophic efficiency (meaning the proportion of the trophic group's biomass consumed by a predator or caught by fisheries).

The second equation represents the mass balance of the compartment, i.e., the inflows are equal to the sum of the outflows of the compartment:

Consumption = production + respiration + unassimilated food

Formally, this equation for a functional group *i* and a predator *j* (*j* being a predator of *i*) can be written as:

$$B_i \times (Q/B)_i = B_i \times (P/B)_i + R_i + U_i \quad (2)$$

where R is the respiration ($t.km^{-2}$) and U is the unassimilated food rate.

The models are then balanced by adjusting the EE when it is greater than 1. Indeed, the EE represents the part of the group production that is consumed or fished, so it cannot be higher than 1. The EE of each functional group was adjusted by modifying the predation control in the diet composition matrix.

2.3. The "Current" model, based on data from 2007–2016

2.3.1. Structure

The "Current" model developed in this paper is composed of 52 compartments ranging from detritus to mammals and seabirds. Among these, 44 compartments, corresponding to species indigenous to the Bay of Biscay, were taken from a previous Ecopath model (Moullec et al., 2017), itself based on a model by Lassalle et al. (2011). These two models differ by their currency: wet weight for the former and carbon for the latter. We used data from both models. Indeed, Moullec et al. (2017) used the values from Lassalle et al. (2011), but chose to give their biomass in wet weight $t.km^2$, as did we. We primarily used the data from Lassalle et al. (2011), except for those in kgC.km, for which we used the values from Moullec et al. (2017), who converted those from Lassalle et al. In addition, we performed some corrections in the composition of fish trophic groups and fisheries. Marine

mammals are divided into two groups according to their size. Seabirds are also divided into two groups, according to their feeding strategies. There are 21 groups of fishes: two groups of chondrichthyans (large piscivorous sharks and small sharks and rays), 11 monospecific groups of fishes targeted by fisheries (seabass, blue whiting, hake, whiting, megrim, sole, plaice, horse mackerel, sardine, anchovy, and pout) and eight multispecific groups: anglerfishes (two species), mackerels (two species), flatfishes (benthos feeders), demersal benthos feeders, demersal piscivores, demersal planktivores, pelagic piscivores, and pelagic planktivores. Cephalopods are separated into two groups: benthic and pelagic. There are eight benthic invertebrate groups (Norway lobster, lobsters/crabs, shrimps, carnivorous and necrophagous benthic invertebrates, subsurface deposit feeding invertebrates, surface suspension and deposit feeders, benthic meiofauna, and suprabenthic invertebrates). Zooplankton are divided into three groups according to their size: microzooplankton (<200 µm), mesozooplankton (200–2000 µm), and macrozooplankton (>2000 µm). Phytoplankton are divided into two groups (small and large), in addition to a primary benthic producers group. There are also groups for bacteria, detritus, and discards.

In addition to these 44 compartments, we considered 8 groups of NIS fishes, which were not included in the two previous models (Lassalle et al., 2011; Moullec et al., 2017). They are composed of three monospecific groups of fishes targeted by fisheries in their original habitat and that would potentially be targeted by the Bay of Biscay fisheries (hake, *Merluccius senegalensis*; horse mackerel, *Trachurus trecae*; and gilt sardine, *Sardinella aurita*) and five multispecific groups (flatfishes, demersal benthos feeders, demersal piscivores, pelagic piscivores, and pelagic planktivores). Potential environmental niche models run by Le Marchand et al. (2020) predicted the arrival of 57 NIS in the study area by 2050 under the IPCC RCP8.5 scenario. The NIS modeled in the present study are the same as those modeled by Le Marchand et al. (2020) (Table S1 in the Supplementary data). These species were selected because their current distribution areas are limited to northwest Africa and are thus most likely to arrive in the Bay of Biscay.

NIS groups have the same preys and predators as those already present in the Bay of Biscay, which we have named “mirror groups” in this study. Their diet proportions are identical to their mirror groups.

The consistency of the Current model was checked with the Ecopath PREBAL tool (Link, 2010) (Figure S2 in the Supplementary data).

2.3.2. Inputs in the Current model

The current biomass of monospecific fish groups targeted by fisheries were calculated from total biomass values given by Ifremer and reported in t.km² (Ifremer 2021), and averaged over the 2007-2016 period. Due to a lack of data, the current biomass of the six multispecific fish groups were estimated by Ecopath using an EE of 0.8 for the pelagic piscivorous group and of 0.95 for the other groups (Table S3 in the Supplementary data). The current biomass of large piscivorous sharks and small sharks and rays were estimated by Ecopath with EE

values of 0.6 and 0.8, respectively (Moullec et al., 2017). The diet matrix was obtained from previous Ecopath models of the Bay of Biscay (Lassalle et al., 2011; Moullec et al., 2017).

To maintain the same structure for the different models, because ENA indices are sensitive to model topology (Fath et al., 2013), the NIS were considered in the Current model with a biomass close to 0 (i.e., 0.0001t.km^{-2}, Table 1). The diets of the NIS multispecific group were the same as for their current mirror groups, due to a lack of information on the diets of those species. The diets of the three monospecific NIS groups were compiled from Fishbase (Froese and Pauly, 2021). The NIS group contribution to the diet of their predators was kept very low.

The P/B and Q/B parameters were updated for all fish groups. The P/B ratios for a fish species *i* were calculated with the empirical equation (Allen, 1971; Pauly, 1980) (Table S3 in Supplementary data):

$$P/B = M_i + F_i = (K_i^{0.65} \times L\infty_i^{-0.279} \times T^{0.463}) + (Y_i / B_i) \quad (3)$$

where K is the growth parameter from the Von Bertalanffy growth function (year^{-1}) for each species (Froese and Pauly, 2021), L∞ is the asymptotic length (cm), T is the mean temperature (°C) over the Current model period (i.e., 2007–2016), Y is the yield (kg.year^{-1}) and B is the biomass (kg.year^{-1}). The temperature assigned depends on the species' vertical habitat, which was provided by Le Marchand et al. (2020): 9.74°C for benthic and demersal (bottom temperature), 11.66°C for benthopelagic (mean water column temperature), and 12.26°C for pelagic species (surface temperature).

For all fish groups, the Q/B ratios were calculated for a species *i*, with the empirical equation (Palomares and Pauly, 1998) (Table S3 in the Supplementary data):

$$Log_{10}(Q/B) = 6.37 - 1.5045 \times \log_{10}T' - 0.168 \times \log_{10}W\infty_i + 0.1399 \times Pf + 0.2765 \times HD \quad (4)$$

where T' is the mean temperature of seawater calculated by 1000/(T + 273.75), W∞ is the asymptotic weight (g), and Pf and HD are two dimensionless variables (Pf = 0 for herbivorous and detritivorous species, 1 for others; HD = 0 for carnivorous species, 1 for others).

As ENA indices are sensitive to model topology (Fath et al., 2013), the topology of all models was standardized. So, the eight NIS groups were considered in the Current model. However, their biomass was close to 0 (i.e., 0.0001t.km^{-2}, Table 1). The diets of the three monospecific NIS groups were compiled from Fishbase (Froese and Pauly, 2021). Their proportion in their predator's diet was kept low in the Current model, given the low biomass (due to absence) of the group. The P/B and Q/B ratios of the NIS monospecific groups were calculated using equations (3) and (4). For the five NIS multispecific groups (i.e., NIS flatfishes, NIS demersal benthos feeders, NIS piscivores, demersal planktivores, and NIS pelagic planktivores), some

of the species in the groups had not been sufficiently documented to calculate the Q/B. So, the choice was made to use the default P/Q ratio of 0.25 instead (Table S3 in the Supplementary data) (Christensen et al., 2005).

Depending on the pertinence of the data they relied upon, the biomass for other EwE functional groups were taken from Lassalle et al. (2011) and Moullec et al. (2015). The detailed information is provided in Table 3 in the Supplementary data.

2.3.3. Fisheries

Landings data were obtained from the International Council for the Exploration of the Sea (ICES; http://ices.dk/marine-data/Pages/default.aspx) for the period 2007 to 2016. To obtain a more realistic Ecopath model, we integrated the 10 main French fleets operating in the area: bottom trawlers targeting demersal fishes, purse seiners, bottom trawlers targeting Norway lobster, gillnetters larger than 15 meters, pelagic trawlers targeting small pelagic fishes, gillnetters smaller than 15 meters, pelagic trawlers targeting demersal fish, long-liners and line vessels, pelagic trawlers targeting tuna, and Danish seine. Other European fleets were also included, mostly from Spain (29% of catches from foreign ships), the United Kingdom (10%), and Belgium (6%). This information was included in the ICES data.

The proportions contributing to the landings by each fleet were calculated from OBSMER reports (Fauconnet et al, 2011; Dubé et al, 2012; Cornou et al, 2013; 2015a; 2015b; 2016; 2017; 2018). ICES data provided the total biomass caught for each species per year. We applied the percentage calculated from OBSMER to the ICES data and obtained for the total biomass of each Ecopath group caught by every fleet from 2010 to 2016. The landings inputs were annual means of these results.

Discards were calculated similarly to landings. Indeed, OBSMER reports include the discard rates for each species and each fleet, from 2010 to 2016. These rates were applied to the ICES catches to obtain annual mean discards over this period.

2.4. Projections

To study the effects of NIS arrivals, we developed a comparative approach by creating five other Ecopath models based on different community changes caused by the arrival of NIS, compared with the current situation (2007–2016). We built these models for the mid-century period (2041–2050) under the IPCC scenario RCP8.5. While the previous version of the work conducted by Le Marchand et al. (2020) was based on both RCP2.6 and RCP8.5, we chose to focus only on the latter. Including RCP2.6 would have considerably increased the number of models. Additionally, the aim of our study was to explore the effects of NIS arrival on native communities, which would be limited under scenario RCP2.6 according to the results from Le Marchand et al. (2020). Thus, we therefore chose to only work with RCP8.5. Into these models, we integrated the impacts of climate change on Bay of Biscay species by

considering (i) the evolution of fish and cephalopod biomass (based on Chaalali et al., 2016) due to the projected evolution (gain or loss) of their suitable habitat (calculated in Le Marchand et al., 2020); and (ii) the changes in the organisms' production and consumption. The five hypotheses of the future evolution of the Bay of Biscay food web illustrate both climate change effects and variation in NIS biomass.

2.4.1. The common basis of the five future models

The five hypotheses simulate progressive variation of the NIS biomass, which is the only parameter to change between the five models. The common basis of the five hypotheses integrates the effects of climate change on fish and cephalopod distributions predicted for the mid-century under RCP8.5 as presented in the previous section.

Future biomass: Species that are projected to show no range shift maintain the same biomass as in the Current model. For the species that are projected to undergo a range loss (Le Marchand et al., 2020), a proportional reduction in biomass is applied according to the reduction in their potential environmental niche (called "ecological niche" in Le Marchand et al., 2020) by 2050 under RCP8.5 (see Chaalali et al., 2016): anglerfishes (-3.12%), whiting (-17.15%), megrim (-3.75%), plaice (-9.73%), flatfishes (-4.89%), demersal benthos feeders (-0.21%), demersal piscivores (-18.64%), pelagic planktivores (-1.21%), and sharks and rays (-0.07%) (Table S4 in the Supplementary data).

The biomass values of cephalopods, benthic invertebrates, zooplankton, phytoplankton, and bacteria estimated by the Current model were used as inputs for the five future hypotheses without any changes, since changes in their potential environmental niches were not considered in this study.

Future P/B and Q/B: The future P/B and Q/B ratios of fishes were calculated using equations (3) and (4) and considering the water temperature projected by mid-century under RCP8.5. The latter has already been calculated by Le Marchand et al. (2020), based on information taken from three general circulation models (GFDL, IPSL, and MPI) (Taylor et al., 2012). The temperature depth was integrated to produce values for the different fish habitat depths: 10.03°C for benthic and demersal, 12.34°C for benthopelagic, and 13.03°C for pelagic species. For groups with several species, the P/B and Q/B were averaged and weighted according to the biomass of each species. The resulting P/B and Q/B differed from those of the Current model (Table S5 in the Supplementary data), which integrates the effects of climate change on metabolism.

For cephalopods, benthic invertebrates, zooplankton, and primary producers, we decided to apply the same alterations (+2%) of P/B and Q/B ratios as those observed for fishes. Thus, the differences between current and projected fish P/B and Q/B values were calculated and it appeared that future P/B and Q/B were 2% greater than current values. As a consequence, a 2% increase of the P/B and Q/B was applied to the cephalopods, benthic invertebrates, zooplankton, and primary producers.

Finally, as mammals and seabirds are homeotherms, their P/B and Q/B ratios remained unchanged in the climate change models.

Fisheries: For the future models, we hypothesized that fishing effort would be the same as in the Current model. The NIS were hypothesized to be fished at the same rate and by the same fleet as their mirror group. However, to take into account the European "zero discard" objective, discards were set to zero in the 2050 models for species under quota. Consequently, landed discards were added to the landings inputs.

2.4.2. Specificities of the projection models

The five hypotheses of the future evolution of the Bay of Biscay food web illustrate both climate change effects and variation in NIS biomass.

Model 1 – ClimOnly: No NIS arrive in the Bay of Biscay. This model integrates only the effects of climate change on the species present in the Current model in the Bay of Biscay (i.e., decrease in the biomass of certain fish species due to the reduction of their potential environmental niches and increased P/B and Q/B ratios). For the ClimOnly model, the NIS biomass were set at 0.0001 $t.km^{-2}$ and maintained at fully consumed (EE > 0.95) (Figure 2) (Table S6 in the Supplementary data).

The following four models are based on the conditions of ClimOnly, to which we added NIS parameters.

Model 2 – NISPel: Only pelagic NIS arrive in the Bay of Biscay, as they are expected to shift more rapidly than demersal species in the Bay of Biscay under climate change. For the NISPel model, the biomass of flatfishes and demersal NIS was set at 0.0001 $t.km^{-2}$ and the NIS pelagic biomass was estimated by Ecopath, using an EE of 0.8 for piscivores and 0.95 for other groups (Figure 2) (Table S7 in the Supplementary data).

Model 3 – NISEqual: In this model, we considered that the environmental niches freed by indigenous species are immediately occupied by NIS with same trophic function. The NIS arrivals counterbalance the loss of biomass due to species impacted by climate change in the Bay of Biscay. The biomass values of the main functional groups remain the same as in the ClimOnly model. As the groups impacted by climate change are mainly demersal and benthic species, this hypothesis mostly models the arrival of demersal and benthic NIS. For the NISEqual model, the NIS group biomass values were equal to the biomass reduction of their mirror current trophic groups due to climate change (Figure 2) (Table S8 in the Supplementary data).

Model 4 – NISMax: In this model, there is no restriction on NIS arrivals. The biomass values are not a priori estimated but calculated by Ecopath by balancing the two model equations

((1) and (2)). An EE of 0.8 is applied for pelagic piscivorous NIS and 0.95 for other groups, as we supposed their EE would be the same as those of the indigenous groups (Table S9 in the Supplementary data).

Model 5 – NISInt: This is a conservative option. A preliminary analysis of the potential impacts of NISMax on the NIS biomass level estimate suggested that a good intermediate situation between NISMax and other models would be obtained by dividing the NISMax biomass by five (Figure 2).

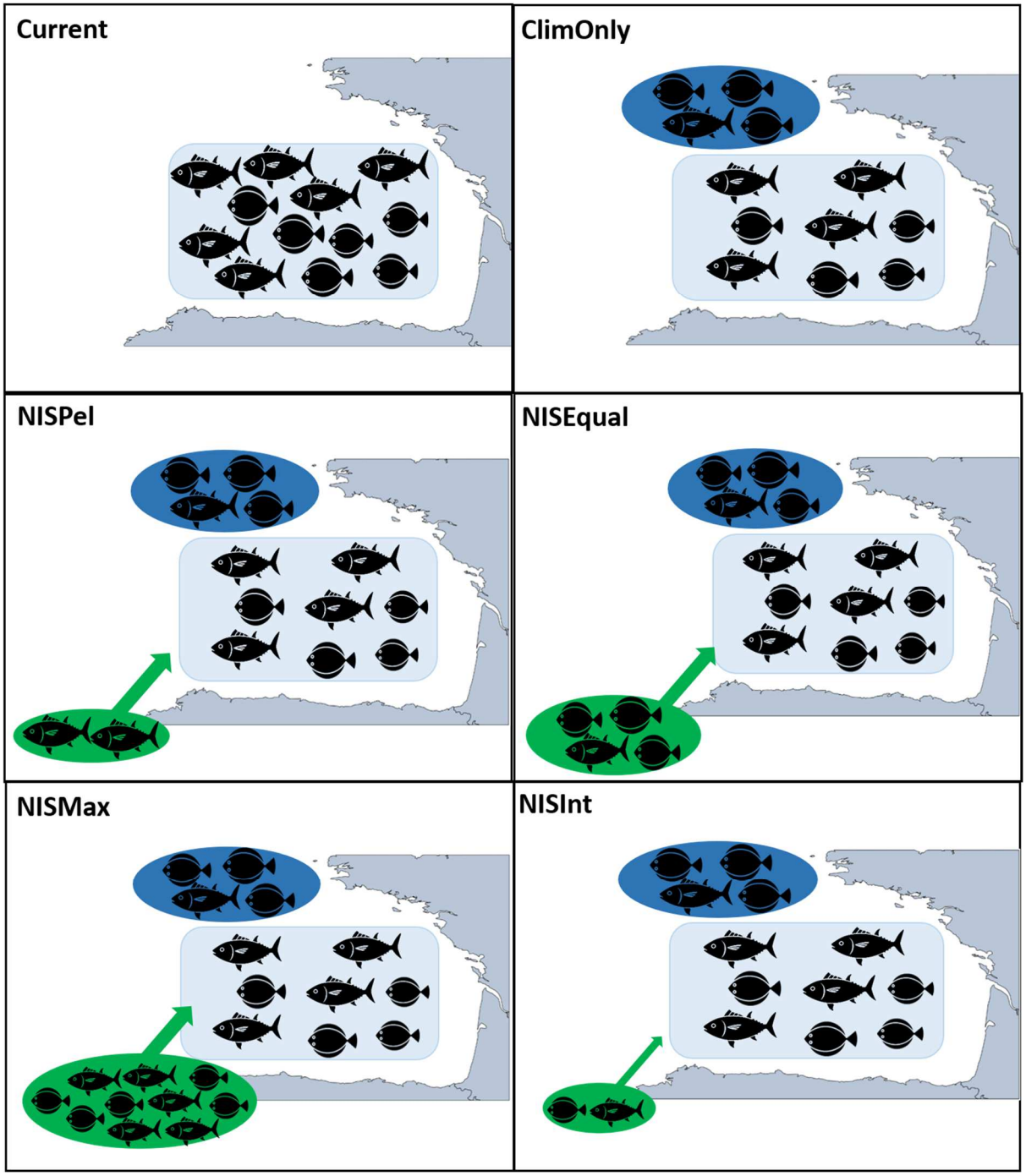

Figure 2: Diagram showing the Current model (2007–2016) and the five projected models (2041–2050). The blue shapes represent the Bay of Biscay species (light blue for species not impacted by climate change and dark blue for species with a reduced biomass due to climate change). The green shapes represent non-indigenous species (NIS). The tuna-shaped symbol represent pelagic and benthopelagic species, the flatfish profile represents benthic and demersal species. The size of the green circle is relative to the NIS biomass.

2.5. ENA

Ecological network analysis (ENA) indices, which reveal the hidden properties of food webs, were used to highlight the effect of climate change and arrivals of new species in the Bay of Biscay. A set of five indices currently calculated in the Matlab routine ENATool

(Guesnet et al., 2015) were selected: Mean Trophic Level 2 (MTL_2), Total System Throughput (TST), Finn Cycling Index (FCI), relative ascendency (A/C), and System Omnivory Index (SOI). In addition, three new indices (Averaged Mutual Information, AMI; Mean Trophic Level 3.25, $MTL_{3.25}$; and Detritivory/Herbivory ratio, D/H) added to this routine were calculated to provide a detailed description of food web structure and functioning (Table 2).

The Matlab routine ENATool takes into account Ecopath input uncertainties. It runs Monte-Carlo simulations to create a set of different versions of one Ecopath model, whose input parameters vary according to the Ecopath pedigree. The pedigree represents the coefficient of variation of every input and varies from 1 (the data are reliable) to 0 (the data estimated by Ecopath are not coherent) (Guesnet et al., 2015) (Table S11 in the Supplementary data). For each model, the ENATool routine created 100 simulations, varying the inputs for biomass and P/B and Q/B ratios, and the diet composition according to the pedigree. All simulations were balanced. For each model, we obtained 100 values for each ENA indicator.

The significant difference between the ENA values of each model was tested by a Kruskal–Wallis non-parametric test, as conditions of normality were not met. Then, the hypotheses were compared with each other using Dunn tests.

For greater clarity in the results, we separated the ENA indices into two groups according to what they reflected: network ENA (TST, FCI, AC, and AMI) and diet ENA (MTL_2, $MTL_{3.25}$, SOI, and D/H).

Table 1: Description of the ENA indices. T_{ij} is the flux from group i to group j; TSTc is the sum of cycling fluxes; TL_i is the trophic level of group i; B_i is the biomass of group i; Q_i is the consumption of group i; OI_i is the omnivory index of group i; D is the fluxes from detritus; Z_i is the import into the system through compartment I; y_i is the output of the system from compartment I; $T_{.j}$ is the flow to compartment j, DCij is the proportion of i in the diet of group j, and H is the flux from primary producers. The * specifies the indicators that were added to the basic ENAtool routine.

Indicators	Definition	Formula	Interpretation of an increase in value
Total System Throughput (TST) /t.year^{-1} Ulanowicz (1986)	Sum of all fluxes in the system	$\sum_{ij} T_{ij} + z_i + y_i$	The overall activity of the system is increasing
Finn's Cycling Index (FCI) % Finn (1980)	Fraction of all system fluxes that are recycled	$\sum_j \frac{\sum_i T_{ij} + z_i}{TST}$	The system has more complex internal links, a better use of energy flowing through the system
Relative ascendency (A/C), no units Ulanowicz (1986)	Quantification of the degree of organization of the system	$-\frac{\sum_{i,j} T_{ij}\, log\left(\frac{T_{ij} TST}{T_{i.} t_{.j}}\right)}{\sum_{i,j} T_{ij}\, log\left(\frac{T_{ij}}{TST}\right)}$	The system has a higher degree of organization, the direct pathways are favored, chain-like
Averaged Mutual Information* (AMI), no units (Hirata and Ulanowicz,	Quantification of the exchange between compartments	$K \sum_{i,j} \left(\frac{T_{ij}}{TST}\right) T_{ij} \log\left(\frac{T_{ij} TST}{T_{i.} t_{.j}}\right)$	The system is more constrained and energy flows through particular pathways

1984)			
Mean Trophic Level 2 (MTL_2), no units (Pauly, 1998)	Mean trophic level of consumers (all species with TL > 2)	$\frac{\sum_i TL_i \times B_i}{\sum_i B_i}$	The proportion of high trophic levels increases in the whole system
Mean Trophic Level 3.25* ($MTL_{3.25}$), no units Shannon et al. (2014)	Mean trophic level of predators (all species with TL > 3.25)	$\frac{\sum_i TL_i \times B_i}{\sum_i B_i}$	The proportion of the higher trophic levels has grown in the predators
System Omnivory Index (SOI), no units (Christensen et al., 1993)	Mean consumer omnivory index	$\frac{\sum_i \sum_j \left[TL_j \times \left(\sum_j TL_j \times DC_{ji}\right)\right] \times log\, T_{.j}}{\sum_i log\, T_{.j}}$	The predators are less specialized. They feed on various trophic levels, this leads to more parallel flows in the system
Detritivory/Herbivory* (D/H) no units (Kay et al., 1989)	Ratio between detritivory and herbivory	$\sum Detritivory / \sum Herbivory$	A greater proportion of the system is supported by detritus

Moreover, we explored ENA index behavior according to the different models using a Principal Component Analysis (PCA). The PCA was performed with the *ade4* package for R Core Team 2019 software (v 3.6.1), with the ENA indices as variables and the models as individuals.

3. Results

3.1. General trends

In the Current model, the trophic levels ranged from 1 to 4.49 (large pelagic sharks). Trophic Level (TL) I was composed of five groups (three groups of primary producers, detritus, and discards) and represented 63.59% of the total biomass. TL II encompassed heterotrophic bacteria, zooplankton, and some of the zoobenthos species, mainly subsurface deposit feeders; it represented 26.76% of the total biomass. TL III was composed of the majority of the fish groups (e.g., demersal piscivores *Trachurus trachurus, Solea solea,* etc.) and represented 9.29% of the total biomass. TL IV corresponded to top predators and represented only 0.96% of the total biomass.

3.2. ENA indices

The first two axes of the PCA (Figure 3) explain 69% of the variance, and only these are presented. The table on the top left of the figure gives information on the percentage contribution of each variable for each of the two dimensions. The first axis (horizontal: 49.2% of the variance) is accounted for by the indices $MTL_{3.25}$ (19.26%), AMI (18.57%), A/C (18.20%), SOI (16.04%), and TST (14.56%). The second axis (vertical: 17.8% of the variance) is accounted for by FCI (50.87%) and D/H (24.58%). All of the models are distinguished on axis

1, with a clear separation of the Current model. The five other models form a group centered on axis 1 and progressively extend toward the right of axis 1. Thus, the Current and NISPel models show opposite positions on axis 1. The Current model stands out by having lower TST, AMI, A/C, and $MTL_{3.25}$ than the other models, but a stronger SOI. Thus, in this model, the lower contribution of trophic level >3.25 seemed to lead energy to flow through multiple parallel pathways that favored omnivory. On the contrary, in the five other models, energy was channeled to particular pathways, limiting feeding on several trophic levels (i.e., omnivory). The models are not really distinguishable from one other on axis 2, although four models (ClimOnly, NISMax, NISInt, and NISEqual) seem to present a slightly higher FCI and D\H ratio.

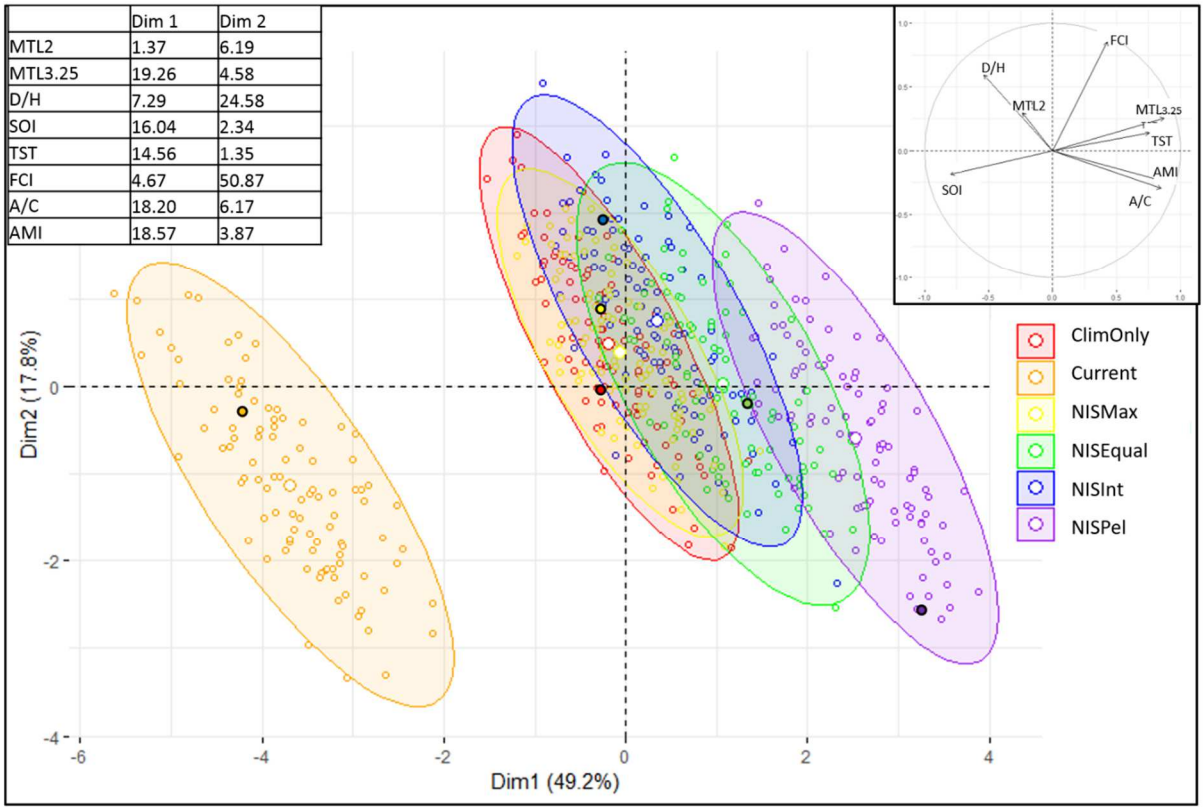

Figure 3: Principal component analysis of the six models (Current, ClimOnly, NISPel, NISEqual, NISMax, and NISInt) and the eight ENA indices (Total System Throughput, TST; Finn's Cycling, FCI; Relative ascendency, A/C; Averaged Mutual Information, AMI; Mean Trophic Level 2, MTL_2, Mean Trophic Level 3.25, $MTL_{3.25}$; System Omnivory Index, SOI; and Detritivory/Herbivory ratio, D/H). Each model includes all 100 simulations performed with ENATool. The solid dots with a black border represent the initial models before applying any changes to parameters based on the ENAtool routine. The white dots represent the average model (i.e., the centroid of each model). The table at the top left shows the absolute contributions of each ENA index for the two axes (in %). The table on the top left gives information on the percentage contribution of each variable for each dimension.

3.2.1. Network ENA

TST increased significantly between the Current model and the projected models (Figure 4, Table 2). The total flux in the system was 6255 (± 261) $t.km^{-2}.year^{-1}$ in the Current

model and increased by 15% on average under the future hypotheses. The projected hypotheses presented significantly different TST values, with the exception of NISEqual and NISInt, which showed similar TST.

The mean A/C ratio in the Current model was 0.223 and increased significantly up to 0.230 under ClimOnly (Figure 4, Table 2). Significant differences were observed between projected models, with the exception of NISPel and NISEqual, which had A/C ratios that were similar and the highest. Mean values of 0.245 and 0.242 were recorded for NISPel and NISEqual, respectively.

The AMI increased significantly between the Current model and ClimOnly (Figure 4, Table 2). All NIS hypotheses showed a significantly higher AMI than Current and ClimOnly models. A significant decrease in the AMI value was observed from NISPel (mean of 1.19) to NISInt (mean of 1.13), with intermediate values recorded by NISEqual and NISMax.

A significant increase of the FCI was obtained with the projected models (Figure 4, Table 2). The Current model showed a significantly lower FCI value than all the other models (mean of 16.85%). The NISInt model had the highest FCI values followed by ClimOnly and NISEqual, which showed similar FCI. The NISPel and NISMax models had intermediate values between the Current model and the other three models.

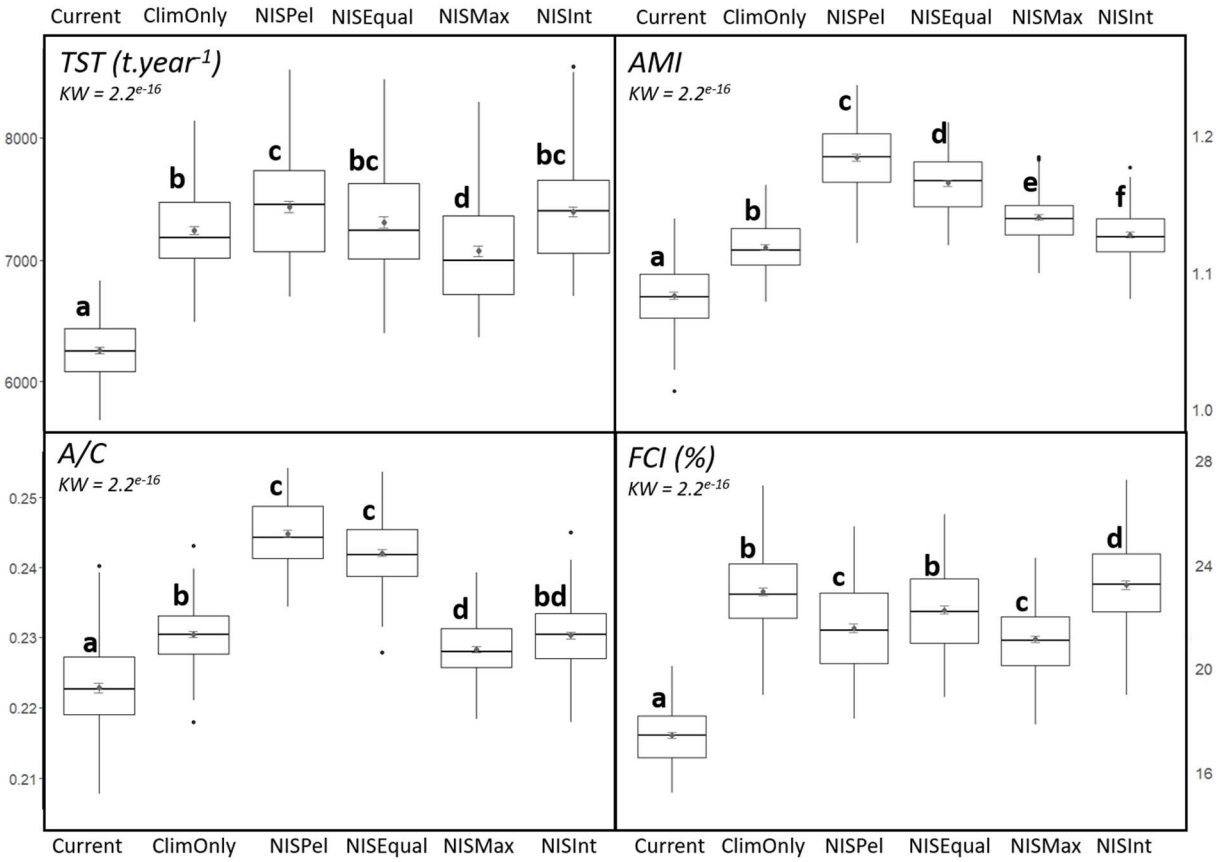

Figure 4: Boxplots of network ENA index values (Total System Throughput, TST; Averaged Mutual Information, AMI; Relative ascendency, A/C; and Finn's cycling, FCI), comparing the Current model and the five projected models (ClimOnly, NISPel, NISEqual, NISMax, and NISInt). The letters correspond to the significance of the differences between the models, based on a Kruskal–Wallis (KW) test (p-value < 0.01) and Dunn tests: two models with a different letter are significantly different. The central dot represents the mean and the standard deviation.

According to these results, climate change is expected to cause system productivity (TST) and recycling (FCI) to increase and to modify the structure of the trophic network (AMI and A/C). Index values varied greatly according to the NIS model. The highest values of AMI and A/C for NISPel and NISEqual imply that in these two models, energy would be forced to flow through direct pathways in order to reach higher trophic levels.

3.2.2. Diet ENA

There was no significant difference in the MTL_2 of the ClimOnly model compared with the Current model (Figure 5, Table 2). A significant decrease of MTL_2 was recorded for the NISPel hypothesis (mean of 2.54) due to the strong increase in biomass of small pelagic fish of low trophic level such as *Sardinella aurita*. A significant increase was calculated for the NISEqual and NISMax hypotheses (means of 2.66 and 2.70, respectively), due to the arrival of non-indigenous demersal benthos feeders and piscivorous fishes, which replaced

528 indigenous species heavily impacted by climate change. The NISInt MTL_2 was slightly higher
529 than the Current and ClimOnly values.

530 The current $MTL_{3.25}$ value (mean 3.48) increased significantly with climate change to
531 reach 3.62 in the ClimOnly model (Figure 5, Table 2). NISPel and NISEqual models showed
532 the highest $MTL_{3.25}$ (means of 3.70 and 3.69, respectively), which can be explained by the
533 increase in fishes of high trophic levels such as tunas for NISPel and demersal piscivorous
534 fishes for NISEqual. The lowest $MTL_{3.25}$ calculated were obtained under the NISInt and
535 NISMax hypotheses (means of 3.61 and 3.65, respectively).

536 The SOI showed a significant decrease between the Current model and all the other
537 projected models (Figure 5, Table 2). There were also significant differences among the
538 future hypotheses. The NISPel model presented the lowest SOI (mean 0.15), whereas the
539 NISEqual model registered the highest among the five future hypothesis values (mean 0.19).
540 However, the NISInt and NISMax values were intermediate (means of 0.16 and 0.17,
541 respectively). The groups with the most marked decrease in omnivory were the top
542 predators (e.g., seabirds, mammals, and sharks) and the pelagic fishes (e.g., planktivores and
543 piscivores) (Table S12 in the Supplementary data).

544 The D/H ratio was significantly lower for the future hypotheses compared with the
545 Current model (Figure 5, Table 2). The decrease in D/H ratio was related to an increase in the
546 flux from primary producers. Detritivory was projected to increase by 4% and herbivory by
547 22% in the future. The increase in herbivory was higher than the increase in detritivory,
548 resulting in a decrease in the D/H ratio.

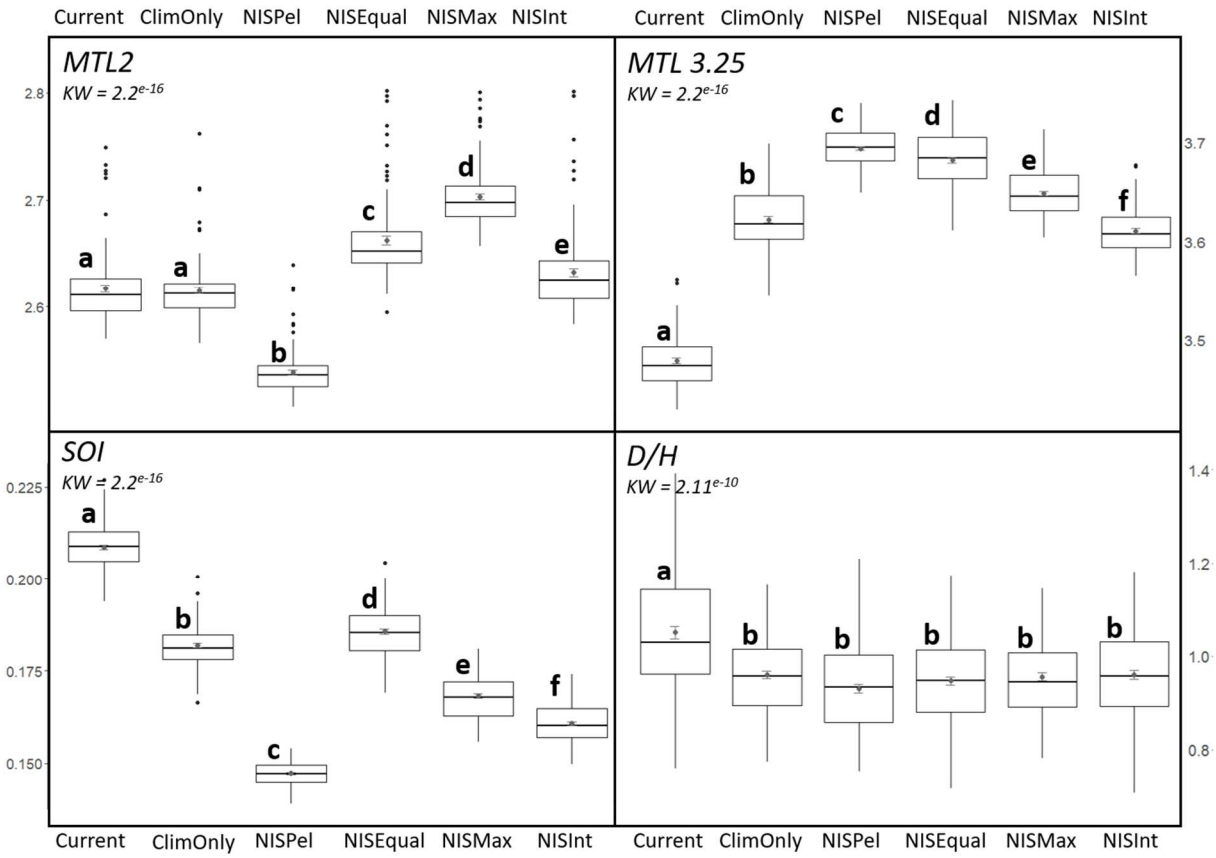

Figure 5: Boxplots of the values of diet ENA indices (Mean Trophic Level 2, MTL_2; Mean Trophic Level 3.25, $MTL_{3.25}$; System Omnivory Index, SOI; and Detritivory/Herbivory ratio, D/H), comparing the Current model and the five projected models (ClimOnly, NISPel, NISEqual, NISMax, and NISInt). The letters correspond to the significance of the differences between the models, based on a Kruskal–Wallis (KW) test (p-value <0.01) and Dunn tests: models with different letters are significantly different. The central dot represents the mean and the standard deviation.

Climate change is expected to affect the relative contribution of primary producers and detritus to the feeding of primary consumers. In addition, the effects of both climate change (i.e., decreased biomass of some groups) and of NIS arrivals would modify trophic interactions, especially by decreasing the mean omnivory (SOI) in a various ways, according to the NIS model. The mean trophic level indices (MTL_2 and $MTL_{3.25}$) showed changes in the community, with variations according to the trophic functions of arriving NIS.

Table 2: Synthesis of trends of ENA indices (Total System Throughput, TST; Finn's cycling, FCI; Relative ascendency, A/C; Averaged Mutual Information, AMI; Mean Trophic Level 2, MTL_2; Mean Trophic Level 3.25, $MTL_{3.25}$: System Omnivory Index, SOI; and Detritivory/Herbivory ratio, D/H), comparing each future model (2041 – 2050) to the Current model (2007 – 2016). The symbol ↗ indicates a significant increase of the index value in the future model, ↘ represents a significant decrease and an equal sign '=' means that the Current model and the future model are significantly identical. A single arrow indicates a slight variation, a double arrow indicates stronger variation and a triple arrow indicates maximal variation.

ENA	ClimOnly	NISPel	NISEqual	NISMax	NISInt
TST	↗↗	↗↗↗	↗↗	↗↗	↗↗
FCI	↗↗	↗↗	↗↗	↗↗	↗↗↗
A/C	↗	↗↗↗	↗↗↗	↗↗	↗↗
AMI	↗	↗↗↗	↗↗	↗↗	↗↗
MTL_2	=	↘	↗↗	↗↗↗	=
$MTL_{3.25}$	↗↗	↗↗↗	↗↗	↗↗	↗↗
SOI	↘↘	↘↘↘	↘↘	↘↘	↘↘
D/H	↘	↘	↘	↘	↘

4. Discussion

In this study, we projected the potential response of the Bay of Biscay trophic network to changes in species composition and relative abundances driven by a rise in sea temperature. Our results can be interpreted on three levels. Firstly, the comparison of ENA indices between the Current model and the ClimOnly hypothesis gives us information about the effects of species distribution range reduction due to climate change and increasing metabolism. Secondly, the comparison of ENA indices between the ClimOnly hypothesis and the four others (i.e., NISPel, NISInt, NISEqual, and NISMax) enables us to examine the consequences of NIS arrivals. Finally, the comparison of ENA indices between the Current model and the four NIS hypotheses reveals the combined effects of biomass decreases of some local species and biomass increases of NIS. Several previous studies have investigated the consequences of the arrival of invasive species (Miehls et al., 2009; Baird et al., 2012; Libralato et al., 2015; Goren et al., 2016) or of climate change (Albouy et al., 2014; Raoux et al., 2018; Bourdaud et al., 2021) in food webs structured by native species. A previous study has dealt with the arrival of non-indigenous species in the Mediterranean sea as a result of climate change (Moullec et al., 2019b). These species are expected to arrive due to a northward or southward shift of their range following an increase in water temperature, but are not necessarily expected to become invasive (Lenoir et al., 2020; Urban, 2020).

4.1. Model limitations

We tried to build our models to be as exhaustive as possible. However, some aspects were not taken into account, even though they could play an important role in predicting the future of the ecosystem. Firstly, the models we used did not integrate the organisms' adaption capability. For example, generalist species might experience a diet shift, which would redesign the trophic network. Moreover, the opportunistic processes of fishes and cephalopods in predation cannot be integrated into Ecopath, as the diet matrix is predefined

and fixed. Thus, this study does not accurately reflect diet adaptability due to community changes. Furthermore, we did not model a decrease in the native species P/B, even if their biomass declined due to climate change. This suggests that these species are currently at their optimum productivity. Based on this assumption, increasing the native species P/B in the future models as we did hypothesizes that the native species could further develop in the Bay of Biscay and could limit the development of NIS by contrasting with a strong competition.The study of NIS arrivals could be improved by the use of Ecosim and Ecospace. The study could also be improved by forcing the lower trophic level food web according to biogeochemical models. This would make it possible to fit the trophic networks with more realistic phytoplankton and zooplankton biomass variation. Indeed, in the study, we chose to model an increase in primary production, which goes against global projections but follows the trend observed in the Bay of Biscay (Chust et al., 2021). However, as the Bay of Biscay is bottom-up controlled (Corrales et al., 2022), it is vital to obtain reliable results on the evolution of low trophic levels. Also, our models suggest that fishing mortalities would remain constant until the mid-century. However, fisheries management is likely to be adapted to the situation (Badjeck et al., 2010; Quentin Grafton, 2010), especially since the increase in temperature would not impact the stocks in the same way depending on whether the species is stenothermal or eurythermal (Serpetti et al., 2017). Also, our method did not integrate the effects of overfishing of some groups, which can favor NIS to the detriment of native species (Saygu et al., 2020). Furthermore, we assumed that the biomass of native species would decrease proportionally to the reduction of their potential environmental niche, however biomass and environmental niches are not necessarily linked. First, a species will not necessarily use its entire environmental niche: the fact that environmental conditions are favorable in one place does not mean that the species will be present there. Second, biomass does not depend solely on environmental parameters but also on trophic and anthropic factors. Finally, we could not integrate the effects of warming on organism recruitment and spawning, although this has been recorded, for example, on herring in the Celtic Sea (Lauria et al., 2012). Such an effect could indirectly impact biomass and productivity. It is also worth noting that sea temperature affects the organism's length and weight, and the growth coefficient k, which are used in the calculation of P/B (Kielbassa et al., 2010).

4.2. The Bay of Biscay trophic network in 2050 under the RCP8.5 scenario

In this section, we compare the Current model with the ClimOnly model. Our results indicate that such ecosystem alterations could increase the quantity of matter flowing through the food web, as suggested by the 15% TST increase by 2050 under RCP8.5 (+0.77°C at the surface). This can, firstly, be explained by the rise in P/B and Q/B. Indeed, despite an observed decrease in total biomass, increasing P/B and Q/B led to higher flux in the system. With the method used in this study, the decline in biomass is due to the decrease in habitat suitability and the increase in P/B and Q/B is due to the rise in sea temperature. This phenomenon is well-known, as marine organisms' metabolic activity is related to

temperature (Bruno et al., 2015; Carozza et al., 2019). Warming water is expected to increase P/B and Q/B ratios (Brown et al., 2004). Indeed, respiration and excretion fluxes are projected to rise with sea warming, as already modeled for small pelagic fishes in the Bay of Biscay (Chaalali et al., 2016). Moreover, we forced an increase in the phytoplankton P/B in our model, leading to a higher net primary production in the Bay of Biscay by the mid-century. Thus a higher quantity of matter supported the whole ecosystem. Although several marine biogeochemical models have forecasted a 3.3%.°C^{-1} mean global loss of net primary production under RCP8.5, associated with lower diatom biomass (Bopp et al., 2005), these results are often derived from global climate models and do not take into account local specificities (Chust et al., 2014). Some authors have made an assumption of increased primary production. For example, an increase in nutrient concentrations, due to high run-off, would lead to higher primary production (Legge et al., 2020). Moreover, Chust et al. (2021) highlighted an observed increase in primary production in the Bay of Biscay over the last two decades.

The intensification of the quantity of matter in the system following temperature increase under RCP8.5 was associated with an increase in recycling index (i.e., FCI), as previously projected by Chaalali et al. (2016), with an increase of 23% in the Bay of Biscay by the end of the century under RCP8.5. A rise in FCI is commonly observed in disturbed ecosystems (Saint-Béat et al., 2015). This increase in FCI values (calculated as the ratio between recycled matter and the TST) despite an increase in TST, means a higher amount of recycled matter. Fath and Halnes (2007) highlighted that flows to and from the detritus compartment are a major part of total structural cycling and an increasing FCI, therefore, results in an increase in detritivory (Fath et al., 2019). Indeed, an increase in detritivory was projected in the Bay of Biscay, although the D/H ratio decreased due to a greater rise in herbivory. The Bay of Biscay could become more dependent on primary production, despite an increase in detritivory. The drop in D/H ratio is also an indicator of stressed ecosystems (Ulanowicz, 1997). In our case, the higher rate of herbivory can be explained by the increase in primary production (+2%) and may also be due to the decrease in biomass of some demersal species, which could result in a higher biomass of groups responsible for herbivory fluxes. Increased herbivory may therefore be due to a combination of both the increase in primary production and the decrease in predation. In addition, the increasing FCI can be explained by the increase of bacterial P/B and Q/B associated with a constant biomass in the future models. This supposes that excess bacterial production is consumed, which contributes to the increase of the FCI. Regarding the European landing obligation (i.e., no discards) that was applied in our projected models, this change did not show any influence on the trophic network structure at the scale of the whole Bay of Biscay ecosystem because its contribution to the current flow from detritus was only 0.021%.

The loss of biomass of some functional groups due to climate change could directly impact the MTL indicators. A constant MTL_2 (TL > 2) associated with an increase in $MTL_{3.25}$ (TL > 3.25) was expected under climate change. This may be explained by the biomass

reduction of some trophic groups in intermediate trophic positions, combined with a constant biomass of top predators (TL > 4) such as pelagic fishes (e.g., tunas) and sharks. Indeed, demersal piscivorous fishes (TL = 3.7) were projected to lose 18% of their potential environmental niche by the mid-century under RCP8.5 (Le Marchand et al., 2020). As a result, we reduced their biomass by 18% between the Current model and the future hypotheses. In the same way, flatfish biomass (TL = 3.4) was reduced by 4%. The decrease of these groups' biomass combined with the biomass stability of the top predators (TL > 4), such as pelagic fishes (e.g., tunas) and sharks, led to increased productivity, resulting in a constant MTL_2 associated with an increase in $MLT_{3.25}$ with warming. We should note that this study did not take into account the evolution of fishing pressure, which could alter the community structure. However, the significant increase of the trophic level of demersal fishes observed in the Bay of Biscay, associated with the higher biomass of high trophic level predators (Arroyo et al., 2019), corroborates our results. Moreover, although the opportunistic predation behavior of fishes and cephalopods cannot be integrated into Ecopath, as the diet matrix is predefined and fixed, omnivory (i.e., SOI) was projected to greatly decrease by the mid-century. This result is probably due to the drop in biomass of some prey as well as of predators. For example, the fall in biomass of demersal benthos feeding fishes could reduce their predation by higher trophic level species and could, thus, decrease the omnivory of their predators (i.e., demersal piscivorous fishes). Indeed, the demersal piscivorous omnivory indicator decreased by 44% under the ClimOnly hypothesis (Table S12 in the Supplementary data). Moreover, it is important to note that the omnivory index is calculated based on the trophic level of prey. Thus, all modifications to prey trophic levels may alter the omnivory index value. The decrease in omnivory was associated with a rise in the relative ascendency. This suggests that parallel pathways (feeding directly or indirectly on a group) tend to disappear. The fall in the biomass of some functional groups could explain this observation. Indeed, energy was weakly channeled to trophic pathways to/from groups whose biomass was altered. As a consequence, other pathways were favored, causing the increase in A/C. The trend in both these ENA indices (i.e., increase in A/C, decrease in SOI) by 2050 under the effect of climate change according to RCP8.5 indicates a system becoming simpler by moving towards a chain-like food web.

Changes with the arrival of NIS

The arrival of NIS altered energy circulation in the system. It amplified the impact of climate change (ClimOnly) on the AMI. The impact on other network properties depended on the nature of this arrival. ENA indicators are known to be sensitive to environmental specificities and physical parameters, making it difficult to compare ENA values among different ecosystems, but efficient for a "before/after" comparison (Niquil et al., 2012). Indeed, ecosystems are distinguished by specific network properties resulting from interactions between organisms and between these organisms and their environment. These properties affect the ecosystem response to a perturbation, hence the diversity of effect on invasive species. First, the A/C index was very sensitive to the arrival of NIS. The arrivals in

721 the NISPel and NISEqual models could lead to higher A/C and AMI values. This means that
722 these two models could increase the full food-web organization and favor direct pathways to
723 reach higher trophic levels with potentially greater efficiency. Concerning FCI, the variations
724 between the NIS hypotheses highlighted the effects of community composition. Indeed, FCI
725 is strongly correlated with the type of community (Baird et al., 2007). It is worth noting that
726 high biomass of pelagic species (i.e., the NISPel and NISMax hypotheses) induce lower
727 cycling rates. In contrast, higher biomass of demersal species (i.e., the NISEqual model)
728 showed high rates of cycling. Finally, the NISInt model with a low biomass change for both
729 pelagic and demersal species does not seem to affect the cycling rates. It is worth noting
730 that the P/B and Q/B values of NIS were different from those of their mirror groups (Table S5
731 in the Supplementary data), as they were calculated separately for the study. There was no
732 trend in the values. The largest contributors to the flow to detritus under the ClimOnly
733 model were microzooplankton (41%), although this proportion is highly dependent on the
734 structure of the trophic network. The major predator of microzooplankton is
735 mesozooplankton. High consumption of mesozooplankton by planktivorous fishes induces a
736 decrease in predation on microzooplankton. This lessens the flow to detritus by small
737 phytoplankton that are the diet of microzooplankton.

738 The arrival of NIS could amplify the effect of warming on the trophic network
739 structure in the Bay of Biscay due to changes in predation controlled by fish biomass. The
740 MTL of both low trophic level consumers (TL > 2) and predators (TL > 3.25) could be affected
741 by changes in trophic composition. For example, NISPel is characterized by a drop in MTL_2 (-
742 3% compared with ClimOnly), due to a massive arrival of planktivorous pelagic fishes such as
743 *Sardinella aurita* and *Trachurus tracae* with a low trophic level (respectively 2.5 and 3.3). It
744 should be noted, however, that the amount of zooplankton consumed by *Sardinella aurita*
745 may have been underestimated in our model, giving it a lower trophic level than other
746 planktivorous pelagic fishes such as *Sardina pilchardus* and *Engraulis encrasicolus*. On the
747 contrary, the $MTL_{3.25}$ was very high (+2% compared with ClimOnly), indicating the arrival of
748 top predators such as tunas. The MTL_2 could increase due to a massive arrival of demersal
749 piscivorous species. The significant decrease in the SOI index suggested that the arrival of
750 NIS could amplify the effect of climate change on changes to the trophic network structure.
751 In the Baltic Sea, the arrival of a new predator, an invasive crab (*Rhithropanopeus harrisii)*, in
752 a bottom-up controlled ecosystem, has been known to deeply impact both lower trophic
753 levels (by a drop in species richness) and pelagic phytoplankton (by a greater biomass) (Kotta
754 et al., 2018). The NISEqual hypothesis proved that a simple change in marine communities
755 could greatly affect trophic functioning. In the Barents Sea, the observed borealization of
756 Arctic marine communities due to the climate-driven expansion of boreal species is
757 reportedly inducing a deep change in the structure of the current Arctic trophic network
758 (Frainer et al., 2017; Pecuchet et al., 2020; Frainer et al., 2021). In Norway, community
759 changes in the sublittoral area due to kelp expansion induced a change in the trophic
760 structure and its associated flows (Paar et al., 2019). Our results highlighted the issue of NIS,

761 which should be considered more frequently in ecosystem modeling. Indeed, not
762 considering this question may affect ecosystem model projections (Bentley et al., 2017).

763

764 *Combined effects and implications for the trophic network*

765 We expected that a decrease in total biomass and trophic functions due to
766 potentially reduced environmental niches under climate change could be offset by the
767 arrival of NIS. However, our results indicate that whatever the biomass and species arriving
768 in the Bay of Biscay with sea temperature rise, some effects could be observed on the
769 trophic networks. Even in the case of NISEqual, in which the functional groups' losses were
770 replaced in terms of quantity, the trophic network was not projected to return to the current
771 structure. The effects of climate change in the marine realm are often studied individually,
772 whereas these effects are more likely to occur in combination, which could have a more
773 profound impact on ecosystems and fisheries (Ainsworth et al., 2011; Halpern et al., 2015).
774 In terms of the combination of different consequences of climate change, our results
775 support the idea that the ecosystem response is more complex when two or more stressors
776 are associated. The case of the NISEqual hypothesis showed that the arrival of NIS of the
777 same trophic function and in the same proportion could not compensate for the effects of
778 the increase in sea temperature.

779 The cumulative effects of both sea warming and the arrival of NIS could lead to less
780 resistant and less resilient ecosystems in the Bay of Biscay. Even though the interpretation of
781 ENA indicators is often complex (Saint-Béat et al., 2015), our results illustrate major trends.
782 According to Saint-Béat et al. (2015), FCI, SOI, and A/C can be used to estimate the response
783 of a system to a perturbation. In our case, the increase in FCI in the projected models is
784 typical of stressed ecosystems. The disruption of initial recycling has a strong impact on the
785 ecosystem due to the large number of indirect effects associated with cycling (Fath and
786 Halnes, 2007). By indirect effects, the authors referred to paths between two compartments
787 of a length greater than 1. As a consequence, changes in cycling can alter pairwise relations
788 leading to a potential impact on ecosystem response to perturbation such as species
789 invasion, extinction as well as climate change. Omnivory enables the system to adapt to a
790 perturbation by shifts in predator diet. Our results show a large decrease in the omnivory
791 index in the future. The ecosystem could thus be most impacted by the decrease or loss of a
792 species or trophic group, as the ability of a consumer to modulate its diet according to the
793 prey present falls. A decrease in omnivory reduces the flexibility of the system and,
794 therefore, makes it more vulnerable to the disappearance or reduction of biomass of a
795 trophic group. In this way, the consequences for the trophic cascade could have a greater
796 impact (Spiers et al., 2016). However, the combined interpretation of omnivory and A/C
797 shaded this conclusion. The future increase of A/C observed brings the system to a state
798 closer to the "window of vitality" of ecosystems, which defines the optimal range of A/C
799 where the ecosystem is the most sustainable (Fath, 2015). A stress in an ecosystem induces
800 a change in its structure and functioning. In our case, the stress induced by the increase in

sea water temperature and the arrival of NIS changes the structure of the trophic network and the way energy enters it. It decreases the capacity of the system to absorb new stresses. The multiplication of pressures on an ecosystem accentuates the consequences of each pressure taken separately (Halpern et al., 2007; Wernberg et al., 2011).

5. Conclusion

This study is timely and important because the cumulative impacts of climate change and non-indigenous species arrivals have rarely been studied in the marine realm. Given uncertainties about non-indigenous species arrivals, simulation through several models was relevant. Indeed, we cannot predict when and which species will enter the area from southern regions under climate change. The models we developed in this study could all represent future realities occurring at different times in the near future. It is possible that NISPel may happen first, then the arrival of demersal with NISEqual and finally the establishment of NIS with high biomass: NISMax. ENA indicators are increasingly used to quantify changes in ecosystems in order to adapt management strategies (Safi et al., 2019). They make it possible to compare a single ecosystem at different levels of change and to compare trends with other ecosystems. The ENATool routine (Guesnet et al., 2015) allowed us to make up for lacking data, especially concerning organism biomass. Our results revealed a negative impact of sea warming on the current trophic network due to the loss of functional group biomass, despite an increase in productivity. The arrival of NIS could imply changes in communities, restructuring the trophic network. Finally, the cumulative effects of both these influences could accentuate trophic network degradation.

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