From species distributions to ecosystem structure and function: a methodological perspective

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Abstract

As species biology and ecology is profoundly influenced by climate, any climatic alteration may have severe consequences on marine pelagic ecosystems and their food webs. It remains challenging to estimate the influence of climate on both structural and functional properties of food webs. In this study, we proposed an innovative approach to assess the propagating effects of climate change on ecosystem food web. The approach is based on a sensitivity analysis of a food-web model, a linear inverse model using a Monte Carlo method coupled with a Markov Chain, in which changes in the values of parameters are driven by external ecological niche model outputs. Our sensitivity analysis was restricted to parameters regarding a keystone functional group in marine ecosystems, i.e. small pelagic fish. At the ecosystem level, the consequences were evaluated using both structural and functional ecological network indices. The approach is innovative as it is the first time that these three methods were combined to assess ecological network indices sensitivity to future climatic pressure. This coupling method was applied on the French continental shelf of the Bay of Biscay for which a food-web model already exists and where future changes in the distribution of small pelagic fish have already been examined through model building and projections. In response to the sensitivity analysis corresponding to an increase in small pelagics production only, our results suggested a more active system with an intense plankton-small pelagics-seabirds chain and an efficient recycling to maximize detritus use in the system in relation with detritus export. All results combined together seemed to be in favor of a system adapting to sustain the tested increase in production of small pelagic planktivores. Finally, regarding the innovative combination of numerical tools presented, even if further investigations are still necessary to get a more realistic view of cumulative effects resulting from one given pressure (or more) on a food web (e.g. altering different biological compartments at the same time), the Ecological Network Analysis indices values showed a higher variability under the scenarios of change. Our study thus pointed out a promising methodology to assess propagating changes in structural and functional ecosystem properties.

Keywords: climate-induced changes; food web; small pelagics; linear inverse model; Ecological Network Analysis; ecological niche.

1. Introduction

The effects of climate change on biological and ecological systems is incontrovertible (Doney and Sailley, 2013; Beaugrand et al., 2015a) and is likely to lead to unexpected modifications in ecosystems functions (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Beaugrand et al., 2009) and associated services for humankind, with strong socio-economic implications (Halpern et al., 2008). In the context of human-driven climate change, these modifications of ecosystem structures, functions, and status are at least partly related to strong alterations of lower trophic levels such as primary producers, primary consumers or planktivorous organisms in aquatic environments (Parmesan and Yohe, 2003; Parmesan, 2006). Different responses have been documented, including physiological effects of climate change on organisms (Arrhenius, 1889; Magnuson et al., 1979), phenological shifts (Edwards and Richardson, 2004) and potential changes in species spatio-temporal distributions (Quéro et al., 1998; Stebbing et al., 2002; Hermant et al., 2010; Alekseenko et al., 2014). However, the propagation of these alterations through the food webs and their consequences on the food-web emerging properties remains poorly understood with only rare examples documented for freshwater and marine systems (e.g. Woodward et al., 2010; Albouy et al., 2013; Chust et al., 2014).

In line with these major issues, our paper proposes a methodology to investigate the propagating effect of climate change on the trophic pathways and the functioning properties of ecosystems. The study case was the Bay of Biscay French continental shelf, with a special emphasis on the consequences of a change in the production of a keystone functional group, i.e. the pelagic planktivorous fish. Here, we proposed for the first time a combination of three numerical methods: (i) An Ecological Niche Model (ENM; Beaugrand et al., 2011; Lenoir et al., 2011) investigating the environmental descriptors driving species distributions to estimate the changes in the production of small planktivorous fish in relation to future climate scenarios; (ii) A Linear Inverse Model using a Markov Chain Monte Carlo method (Kones et al., 2006; Niquil et al., 2012) to determine the consequences of changes in small pelagics production on the carbon flows of the Bay of Biscay French continental shelf food web; and (iii) Calculation of Ecological Network Analysis indices (ENA; Ulanowicz, 1992; Patrício et al., 2004; Baird et al., 2012; Saint-Béat et al., 2015) to assess the propagating consequences of changes in the production of small pelagics on the whole food web. With this ecologically meaningful study case, we are particularly interested in demonstrating whether ENA indices are reflecting the propagating consequences of a change in one compartment balance. Indeed, the recent European directives [e.g. Marine Strategy Framework Directive (MSFD), Water Framework Directive (WFD)] stress the urgent need of development, test, and validation of ecosystem health indicators. This study combining numerical methods allowed exploring the consequences of climate-related changes on the food-web properties and ecosystem status. Moreover, ENA indices (Ulanowicz, 1986) were proposed as 'candidate' indicators for the common biodiversity indicators list of OSlo and PARis Convention [OSPAR] (Niquil et al., 2014a), because they capture well the functional and structural properties of ecosystems (Ulanowicz, 1992; Patricio et al., 2004; Baird et al., 2012; Saint-Béat et al., 2015).

This study aims to propose a numerical approach (i) to assess propagating changes in structural and functional ecosystem properties and (ii) test the sensitivity of candidate indicators to the climate change pressure for the common biodiversity indicators list of the OSPAR Convention.

2. Materials and Methods

2.1. Study area

The study area considered in this work is the French continental shelf of the Bay of Biscay (between the 30m- and 150m-isobaths), a Gulf of the North-East Atlantic Ocean located off the western coast of France and the northern coast of Spain (48.5°N - 43.5°N and 8°W - 3°W; Figure 1). This system is hydrodynamically complex, being influenced by upwelling events, coastal run-off and river plumes, seasonal currents, eddies, internal waves, and tidal fronts (Planque et al., 2004). The supply of freshwater is mainly provided by 5 rivers: the Loire, the Garonne–Dordogne, the Adour, the Vilaine, and the Charente. All these hydrodynamic processes are known to affect species populations (Varela, 1996; Lampert, 2001; Hily et al., 2008). Ecosystem dynamics is also driven by anthropogenic pressures, the most important being the multifleet fishery operating in the Bay of Biscay (Hily et al., 2008; Rochet et al., 2012). In this respect, the study area is composed of ICES divisions VIIIa and VIIIb (ICES; www.ices.dk) and has a total surface area of 102,585 km^2.

2.2 The Bay of Biscay French continental shelf LIM-MCMC model

This study was based on a Linear Inverse Model used to estimate processes difficult to measure in the field, especially for large ecosystems, and, when combined to ENA indices, characterize the ecosystem status of the Bay of Biscay French continental shelf and its associated structural and functional properties (Chaalali et al., 2015) under varying environmental conditions. The structural properties refer to the network of interactions (i.e. presence or absence of pathways and pathway values) linking the species or groups of species, whereas the functional properties correspond to the emergent properties describing how the carbon flows through ecosystem boundaries.

The LIM was built as a combination of mass-balance equations (and potential *in situ* measures of flow expressed as complementary equations) and inequalities which constrain flow values. In most cases, constraints were based on the ecophysiology of the species making up the model compartments (Niquil et al., 2012). LIM food webs are described as linear functions of flows constrained between maximal and minimal boundaries and estimated from empirical data. As the system of equalities is underdetermined, infinity of different solutions exists. The Markov Chain Monte Carlo (MCMC) approach coupled with LIM allows retrieving a large set of solutions of flow estimates from the multidimensional space of all possible solutions (Van den Meersche et al., 2009). In this study, 1 million of values for each of the 124 carbon flows were estimated by the LIM-MCMC. The species considered in our LIM-MCMC model was the same as those of the Ecopath model by Lassalle et al. (2011) with the exception of two species of tuna (added in the LIM-MCMC). Among the differences between the two models, an important one was structural and corresponded to the reduction in the number of functional groups from 32 to 18. More details can be found in Chaalali et al. (2015), notably the empirical data sources used for network construction and model parameterization (e.g. *in situ* measures of flow, ecophysiological constraints, and biomass). The development of food-web models was made possible by the two successive phases of the French coastal environmental research program (PNEC 1999-2003 and 2004-2007) that both included a specific worksite on the Bay of Biscay and that thus greatly contributed to fill the gaps that existed in the data concerning this area.

The LIM-MCMC represented an average year between 1994 and 2005. Small pelagics in the Bay of Biscay were composed of the European anchovy, *Engraulis encrasicolus*, the European pilchard, *Sardina pilchardus*, and the European sprat, *Sprattus sprattus*. All three species were grouped into a single functional compartment named “pelagic planktivorous fish” in the LIM-MCMC model according to their mainly planktivorous diets.

2.3. The Ecological Niche Model applied to small planktivorous fish

The ecological niches and the spatial distributions of the European anchovy, the European pilchard, and the European sprat were estimated by the Non-Parametric Probabilistic

Ecological Niche (NPPEN) model (Beaugrand et al., 2011). The NPPEN model is described in full details in Beaugrand et al. (2011) as well as in subsequent articles presenting different study cases (e.g. Lenoir et al., 2011; Chaalali et al., 2013a; Frederiksen et al., 2013; Raybaud et al., 2013; Goberville et al., 2015; Raybaud et al., 2015). The NPPEN model only requires presence data and uses the Mahalanobis distance, which allows the consideration of the correlations between explanatory variables (Farber and Kadmon, 2003). Based on presence-only data, the NPPEN model calculates the probability of occurrence of a species as a function of some key abiotic variables. In the Euclidean space of the niche, the probability of occurrence is calculated for each combination of environmental variables. Then, an interpolation is made to project the niche into the geographical space.

More practically, in this study, we used NPPEN models outputs and projections provided during the BIODIMAR project (www.biodimar.org). The first step of NPPEN modeling had consisted in the identification of the abiotic variables that condition the most the small pelagics' ecological niches to model species probabilities of occurrence for the 'reference' period. Four variables for which empirical data must be available at the species distribution scale were tested and the NPPEN models were run with eleven combinations of variables to assess the ability of each combination to reproduce the observed spatial distribution (Lenoir and Beaugrand, 2008; Lenoir, 2011; Raybaud et al., submitted). For each of the three small pelagics, the best combination was selected based on the Boyce Index (CBI; Hirzel et al., 2006), a modification of the Boyce index (Boyce et al., 2002) especially designed for presence-only models (Braunisch and Suchant, 2010). This index is based on a moving window analysis on the predicted-to-expected (P/E) frequency curve and uses the Spearman rank correlation coefficient to measure the monotonic increase of the curve. Values of CBI vary from -1 for an inverse model to 1 for a perfect prediction. Values close to zero indicate a random model. The abiotic variables retained in the models were the annual Sea Surface Temperature (AVHRR-SST data for the period 1982-2009; Casey et al., 2010) and the bathymetry (bathymetric data from the “Smith and Sandwell Global Seafloor topography”; Smith and Sandwell, 1997).

To establish projections of the future species probabilities of occurrence for the end of the century (2090-2099), we used SST outputs from an Earth System Model : IPSL-CM5A-MR (Bopp et al., 2013) and the latest generation of climate scenarios called RCPs (Representative Concentration Pathways, (Moss et al. 2010)), which are a part of the fifth Intergovernmental Panel on Climate Change (IPCC) assessment report (Taylor et al., 2012). Here, we used both the intermediate scenario RCP4.5 (a scenario that stabilizes radiative forcing at 4.5 $W.m^{-2}$ in 2100 and projects a global temperature increase of 2°C) and the ‘business-as-usual’ scenario RCP8.5 (a rising radiative forcing pathway leading to 8.5 $W.m^{-2}$ in 2100 and a global temperature rise by more than 4°C (Knutti and Sedlacek, 2012)).

Finally, from two matrices (latitude x longitude) of probabilities of occurrence (for the reference period, $P_{reference}$; and each RCP scenario tested, P_{RCP}), we calculated coefficients of change for each geographic cell. These coefficients that vary between -1 and 1 were assessed using the following formula:

$$C = \frac{P_{reference} - P_{RCP}}{P_{reference}}$$

As a coefficient value was computed per geographic cell, mean coefficients ($\bar{C}$) were then calculated following the latitudinal gradient (i.e. by matrix rows). Both a maximum and minimum mean coefficients ($\bar{C}$) were used to integrate the variability of NPPEN estimates into the LIM-MCMC model for each RCP scenario as presented below.

2.4. Forcing of the Bay of Biscay LIM-MCMC model

A single change was applied to the LIM-MCMC model parameterization presented in Chaalali et al. (2015). The pelagic planktivorous fish production was modified according to simulations from the NPPEN inputs. Only a single perturbation was applied as the main question of the present study was to assess the capacity of ENA indices to integrate changes at the population level. Nonetheless, this perturbation was ecologically meaningful as we selected a functional group demonstrated to be a key compartment of the system and as we applied a change in the compartment parameters in accordance with outputs of ecological niche models.

In the model of Chaalali et al. (2015), the production estimates were calculated by multiplying Production/Biomass (P/B) ratios by biomass estimates for each of the three species and then the production of the functional group was assessed as a sum of each product. Species P/B ratios were the same as in Lassalle et al. (2011). Time series of pelagic fish biomass were obtained from acoustic surveys conducted each spring in the Bay of Biscay (PELGAS IFREMER cruises) between 1994 and 2005. Inter-annual variations in species biomass across the period were used to calculate minimum and maximum production for the functional group (as the species P/B varies little in comparison to inter-annual biomass variability).

Here, we hypothesized that the $\bar{C}$ values estimated from the NPPEN simulations would most likely reflect a change in species biomass. We based on the ecological niche theory suggesting a maximum of species density associated to a specific range of environmental descriptors (Hutchinson, 1957). Higher probabilities of species occurrence predicted by NPPEN simulations suggest more favorable environmental conditions and, from a mechanistic point of view, a higher species reproductive success and population size, and therefore biomasses. We thus used this ecological assumption instead of considering an arbitrary value of change in biomass. Moreover, this relationship was already verified for lower trophic level organisms, e.g. copepods, at species level, such as for *Calanus spp.* (Helaouët et al., 2013) and *Acartia spp.* (Chaalali et al., 2013a; 2013b).

A positive $\bar{C}$ value corresponded to a decrease in species mean probability of occurrence between the reference and future situations. To translate this probability change into a future biomass and then production, the species biomass was multiplied by $1 - \bar{C}$ (with $\bar{C}$ being comprised between 0 and 1). Inversely, for a negative $\bar{C}$, an increase in species average probability of occurrence was predicted by the NPPEN model. Species biomasses were also transformed using $1 - \bar{C}$ but this time, $\bar{C}$ was comprised between 0 and -1, leading to higher biomass estimates.

For each small pelagic species, the minimum $\bar{C}$ was multiplied by the minimal biomass estimated by PELGAS acoustic survey and inversely. By computing each species minimal and maximal future biomasses, new boundaries for the pelagic planktivorous fish production were calculated taking the two opposite extremes among these 6 values (i.e. 2 boundaries x 3 species) and the model was run with these new constraints on the production term. We applied this procedure to better integrate the NPPEN-predicted decrease of pilchard distribution range (by reducing the most the functional group production in the LIM-MCMC using the minimum future pilchard biomass – acting on the production minimal boundary), and the expected increase of European anchovy and sprat distribution ranges (by increasing the most the functional group production in the LIM-MCMC using the maximum future anchovy and sprat biomasses – acting therefore on the production maximal boundary) (Figure 2A). P/B ratios were left unchanged compared to the reference situation as no quantitative and precise information exist on their potential evolution under climate change.

Even if the present sensitivity analysis realized on the LIM-MCMC model was only based on a single modification of a given flow, i.e. the production of small pelagic fish, and therefore did not aim to be a ‘realistic’ view of climate change impacts at population level, all the group intrinsic flows (i.e. respiration, egestion, predation on and by this group) were modified accordingly as they were, by construction, all related to each other (i.e. mass conservation hypothesis) (see Chaalali et al., 2015 for more details). Thus, the temperature incidence on the whole species metabolism (not only its production) was implicitly considered. One million of iterations were calculated for the 1994-2005 period and for the two RCP scenarios (2090-2099). The choice was made to perform one million of iterations in view of the quality of the exploration of the solution space by the mirror technique (i.e. graphical analysis) (Kones et al., 2006; Niquil et al., 2012).

2.5. Ecological Network Analysis

Ecological Network Analysis (ENA; Ulanowicz, 1986) was used to compute several indices to compare the function of the Bay of Biscay French continental shelf food web nowadays (1994-2005) and in the future (2090-2099), after climate alterations on pelagic planktivorous fish production.

Various ENA indices were calculated (Table 1), namely Total System Throughput (T..), Internal Ascendency (Ai), Internal Capacity (Ci), Internal Relative Ascendency (Ai/Ci), Average Path Length (APL), Finn’s Cycling Index (FCI), System Omnivory Index (SOI). The Total System Throughput (T..) is computed as the sum of all flows in a food web and therefore corresponds to the system activity (Ulanowicz, 1980; 1986; Latham, 2006). The internal ascendency (Ai) describes the ecosystem development (Ulanowicz and Abarca-Arenas, 1997), whereas the internal capacity (Ci) describes the system maximal stage of development, and corresponds to the upper limit of the internal Ascendency (Ai). The internal relative ascendency (Ai/Ci) provides a relative measure of the degree of organization of a food web based only on internal flows. The Average Path Length (APL) is defined as the average number of steps along the shortest path for all possible pairs of network nodes. Finn (1980) proposed an index of the importance of recycling activity (FCI) corresponded to the proportion of the sum of internal transfers plus imports involved in cycles (i.e. loops are pathways beginning and ending in the same compartment). According to Ulanowicz (1986), the System Omnivory Index (SOI) generally reflects the complexity of the linkages within an ecosystem (in terms of organization).

A MATLAB routine, adapted from the one developed by Carole Lebreton and Markus Schartau (GKSS Research Center, Geesthacht, Germany), was used to compute one ENA index value per vector of flow estimates from the LIM-MCMC, leading for each ENA index to 1 million values.

The Detritivory/Herbivory (D/H) ratio, calculated as the sum of flows originating from both detritus and Dissolved Organic Carbon (DOC) compartments divided by the sum of flows from phytoplankton, was also calculated. The D/H ratio measures the relative importance of detritivory and herbivory activity in a given system (Ulanowicz, 1992).

The use of the LIM-MCMC approach allowed obtaining a likelihood distribution for each flow and for ENA indices, based on one million of iterations. As a result, descriptive statistics such as mean, minimum, maximum, and standard deviation values can be computed for each flow and ENA index.

2.6. Comparison of flows and ENA indices between periods

The general distribution pattern of flows estimated by the three LIM-MCMCs (one for the reference period “1994-2005”, and the two other for the RCP scenarios) was first assessed with a barplot including all estimated flows. The main changes in the food web were graphically investigated by searching for the flows with a noticeable change in response to the climate-induced changes in the production of pelagic planktivorous fish (i.e. the two RCPs). These changes in flow estimates were also statistically analyzed using a comparison of flow distributions between the reference period 1994-2005 and the RCP 4.5, and then the RCP 8.5. The statistical analysis can be divided into three steps: (i) For a given flow, the mean value of the flow for each of the two situations (i.e. reference and future under climate change) was calculated; (ii) Scenarios were considered by pairs (e.g. reference-RCP 4.5 or reference-RPC 8.5). For the scenario having the distribution with the lowest mean, the quantiles 95, 90, 80, 70 and 65% were calculated. For the distribution with the highest mean, the quantiles 5, 10, 20, 30 and 35% were computed. (iii) Then, a test was performed to assess how much distributions were overlapping. For example, at the 95%-5% interval, an overlap took place when the quantile 95% of a distribution was superior to the quantile 5% of the other distribution (Figure 2B). The levels of significance are fully described in Figure 2.

The values of the ENA indices estimated by the three LIM-MCMCs were plotted and also statistically compared, using the same ‘quantile interval’ procedure as described above for flows.

3. Results

In the LIM-MCMC under the RCP 4.5 and the RCP 8.5, an increased interval was applied on the boundaries of the production of pelagic planktivorous fish. Values switched from [75 –

475] $kgC.km^{-2}.y^{-1}$ for the reference period “1994-2005”, to [72 - 486] $kgC.km^{-2}.y^{-1}$ under RCP 4.5, and to [67 - 536] $kgC.km^{-2}.y^{-1}$ under RCP 8.5.

The general pattern of mean flow estimates from the three LIM-MCMCs was graphically comparable (Fig. S1 and Table S1). Considering the highest mean flow estimates, all models presented a high gross primary production (flow number 1 in supplementary material) with estimated mean values comprised between $2.4 \bullet 10^5$ kgC.km-2.y-1 and $2.9 \bullet 10^5$ kgC.km-2.y-1 for the reference period and for the model under the RCP 4.5 respectively (Table S1). The other highest flows identified in the different food webs were the same and were mainly related to phytoplankton sedimentation (2), or to bacterial and detrital processes (e.g. mean DOC consumption by bacteria (98), between $7.7 \bullet 10^4$ and $1.0 \bullet 10^5$ $kgC.km^{-2}.y^{-1}$; mean bacterial respiration (114), between $4.5 \bullet 10^4$ and $6.2 \bullet 10^4$ $kgC.km^{-2}.y^{-1}$) (Table S1). Some differences nonetheless did appear (Table 2). A high mean detritus export (i.e. detrital carbon flows exported outside the ecosystem boundaries) (124) of $8.5 \bullet 10^4$ $kgC.km^{-2}.y^{-1}$ was calculated for the LIM-MCMC under RCP 8.5. It was almost 5 times higher than the estimate for the LIM-MCMC under RCP 4.5 and for the LIM-MCMC for the reference period (Table S1). This difference was “potentially significant” considering the quantiles’ interval method (Table 2). In addition, decreasing trends in detritus dissolution (89), DOC production by bacteria (80), and DOC and detritus consumption by bacteria (flows with number 98 and 86) were estimated, the latter being “potentially significant” (Table 2). No “trends” or “potentially significant” differences were noticed for RCP 4.5 flow estimates compared to reference period flow estimates, except for the consumption of detritus by bacteria (Table 2).

The input flow estimated for the pelagic planktivorous fish increased with the RCP 8.5; the input flow being defined as all the flows entering into a functional group. The mean input flow estimate was $4.3 \cdot 10^3 \pm 0.3 \cdot 10^3$ kgC.km^{-2}.y^{-1} for the reference period *versus* $4.4 \cdot 10^3 \pm 0.3 \cdot 10^3$ kgC.km^{-2}.y^{-1} under RCP 4.5 and $4.9 \cdot 10^3 \pm 0.3 \cdot 10^3$ kgC.km^{-2}.y^{-1} under RCP 8.5 (Figure 3A). Distributions for this flow overlapped at the 80%-20% quantiles interval, meaning a difference in flow estimates between the RCP 8.5 and the two other situations "potentially significant". More specifically, the consumption of macrozooplankton by the pelagic planktivorous fish (mazTOppl flow in Figure 4) presented a "trend" with a higher estimate for RCP 8.5 compared to RCP 4.5 and the reference period and an overlap detected when considering the largest intervals (Figure 4). The analysis of the other flows that were expected as important to interpret the sensitivity analysis performed on climate-induced changes in pelagic planktivorous fish production showed no differences under climate change scenarios (Figure 4).

When looking at the main prey of the pelagic planktivorous fish, the input flows of zooplanktonic groups between the reference period and the one estimated in 2090-2099 with the RCP 8.5 expressed a slight increasing "trend" (Figure 5A), as overlap was detected at the largest quantile interval 65%-35%. When considering prey of prey, a "potentially significant" difference was noticed for the phytoplankton production under RCP 8.5, with overlapping distributions being observed at quantile interval 80%-20% (Figure 5A).

Possibly in response to the increasing productions of planktonic groups (mentioned above), an increasing trend of their detrital production was also predicted by the models (see Table S1 for more details). The predation exerted by seabirds on small planktivorous fish (i.e. flow abbreviation pplTOsbr in Table S1) was also predicted to increase, especially with the RCP 8.5 scenario as an overlapping of flow estimates was also noticed at the 80%-20% quantiles interval suggesting a “potentially significant” difference (Figure 3B). However, the seabirds input flow was not predicted to significantly change despite the increased predation on pelagic planktivorous fish (Figure 3A).

The analysis of the input flows to bacteria, detritus and DOC showed interesting “trends”: a decreasing trend in inputs to bacteria was predicted under the two RCP scenarios compared to the reference period, inputs to detritus under RCP 8.5 had also a lower mean value compared to the two other situations and the same was predicted for inputs to DOC (Figure 5B).

Regarding the ENA indices comparisons, no difference at any quantiles’ interval was observed for the internal ascendency Ai (mean values around [$6.7 \bullet 10^5 \pm 3.5 \bullet 10^4$ to $1.1 \bullet 10^6 \pm 2.0 \bullet 10^5$ $kgC.km^{-2}.y^{-1}$) or the system omnivory index SOI (0.19 ± 0.03 to 0.21 ± 0.03) (Figure 6B, F). Regarding indices related to the system activity and organization (T.., Ci, and Ai/Ci), some “trends” were observed under the RCP 4.5 scenario. When considering APL, FCI, and the D/H ratio, changes were detected for the RCP 8.5 scenario. An important decrease of the ratio of detritivory on herbivory (D/H) was noticed, passing from a mean of 1.2 ± 0.29 (reference period) to 0.8 ± 0.12 (RCP 8.5) (Figure 6G). Oppositely, and for the same RCP scenario, the Finn Cycling Index (FCI) presented an increasing trend reaching an estimate mean value of 0.16 ± 0.02 (RCP 8.5) *versus* 0.13 ± 0.01 for the reference period. One index seemed to respond to both future climate scenarios: the Averaged Path Length (APL) with a mean at 3.42 ± 0.24 for the RCP 4.5, and 3.26 ± 0.19 for the RCP 8.5. An increasing “trend” (RCP 4.5) and a “potentially significant” positive difference (RCP 8.5) of the APL was thus calculated when compared to the reference period (3.13 ± 0.10). One should finally notice the systematic increase in variability (of both ranges between maximum and minimum estimates and standard deviation) for both flows and ENA indices estimates under the tested climate change scenarios (Figure 6).

4. Discussion

4.1. Potential propagating effects of changes in small pelagic fish production on other flow values

The present sensitivity analysis based on the combination of Ecological Niche Modeling, Linear Inverse Modeling, and ENA highlighted plausible changes in the Bay of Biscay food-web features in response to climatic incidence on a single biological compartment production, i.e. the pelagic planktivorous fish. Despite the similar general pattern of flow estimates obtained from the three LIM-MCMC models (i.e. reference period and the two RCP scenarios), respiration flows and egestion values of small pelagics increased in response to the potential increase of temperature (Table S1). These results can be related to the expected more active metabolism of fish under increasing temperature (e.g. Arrhenius, 1889; Brown et al., 2004). In support to the higher nutritional needs of small pelagic fish caused by the increase in their metabolism and production, the production of low (planktonic) trophic levels - especially the macrozooplankton production and gross primary production - increased in the LIM-MCMCs. The supplemental food intake was directly supported by the macrozooplankton only (i.e. increase of mazTOppl flow value). This conclusion was more likely linked to a methodological cause rather than the result of an ecological process. The flows of consumption by small pelagics of other compartments (i.e. phytoplankton, microzooplankton, and mesozooplankton) were constrained by more restrictive inequalities than the consumption flow exerted on macrozooplankton. Owing to a more documented literature existing on the subject, the inequalities on the flows relative to phytoplankton, micro- and mesozooplankton compartments (e.g. respiration, exudation or/and egestion flows) were more constrained and inter-related in the LIM-MCMC models. Consequently, the space of solutions to explore was smaller. On the contrary, a higher flexibility was given to the flow of predation on the macrozooplankton as we found fewer references on this topic. The LIM-MCMC adjusted the nutritional needs of the pelagic planktonic fish compartment by increasing the consumption operated on this group. The resulting increasing macrozooplankton production was in turn supported by an increase in gross primary production.

According to Bopp et al. (2013), the primary production in the Bay of Biscay is expected to follow an opposite trend. Working on 10 Earth System models and 7 marine biogeochemical models, these authors predicted a significant decrease of the Bay of Biscay productivity at the end of the century in a climate change context. However, the biogeochemical models used in their study were typical Nutrients-Phytoplankton-Zooplankton-Detritus (NPZD) models (with varying degrees of complexity) and did not take into account high trophic level components such as planktivorous fish feeding on zooplankton and potentially decreasing the grazing pressure on primary producers. Moreover, complementary predictions of primary production obtained from a regional model would be also needed to assess the quality and reliability of the downscaling from these global models. The increase in primary production predicted here by the LIM-MCMC models could be therefore interpreted as the only possibility for the model algorithm to satisfy the mass-balances in response to the simulated increase in small pelagics production.

The question remains, however, as to whether a (contradictory) decrease in primary production as predicted by Bopp et al. (2013) will be antagonistic with the changes in small pelagics distribution and production predicted by modeling. A complementary set of analysis was already performed but not yet published (Saint-Béat and Chaalali, unpublished data) to assess the consequences of a potential climate-induced drop in the net primary production (NPP) of the Bay of Biscay as predicted by Bopp et al. (2013). The LIM-MCMC model structure remained the same in this new exercise with, amongst other things, small pelagics feeding on plankton. However, small pelagics productions were no longer modified. Only NPP was changed according to plausible climate change scenarios. This additional work following the same methodology suggested a potential discrepancy between the availability of planktonic preys and the fish consumers' needs in the Bay of Biscay with respect to climate change. Indeed, by forcing the LIM-MCMC with lower boundaries of NPP, we observed a decrease in the consumption flows exerted by pelagic planktivorous fish (and therefore in their production; Figure S1). Chust et al. (2014) got to similar conclusions, suggesting a potential future drop in phytoplankton and zooplankton biomass in the Atlantic margin under climate change with an expected trophic attenuation of the entire chain. Their work was based on two distinct meso-scale models, i.e. POLCOMS-ERSEM and ROMS-NPZD. However, these authors nuanced that uncertainties related to the use of single global and regional models implies a need for caution while extending conclusions into high trophic levels.

Another potential propagating effect of the tested pelagic fish production increase was noted and concerned bacteria that appeared to be less consumed by planktonic compartments under future climate scenarios (shifting part of their diet on primary producers). This can be put in relation with a decrease in the relative importance of the microbial loop in terms of total flows involved, particularly under the worst-case scenario RCP 8.5 (Table S1). On the contrary, detritus appeared to gain in importance for the planktonic groups in sustaining their increase of production, especially under RCP 4.5. As a consequence, the changes in the production of small pelagics may transitionally stimulate the detritivory path with fish eating more planktonic preys and planktonic preys consuming detritus in higher proportions under RCP 4.5. But then, under more severe environmental conditions, the detritivory was predicted to be far less intense leading to a strong detritus export outside the ecosystem boundaries. To conclude on this modeling exercise, two scenarios of temperature increase appeared to lead to two distinct system functioning.

At higher trophic levels, regarding the increased predation by seabirds, Luczak et al. (2011), using a long-term series analysis, reached a similar conclusion of potential propagating effect of temperature rise in the Bay of Biscay. This propagating effect took place in the mid-1990s and consisted in the modification of a seabird northern range margin to follow the expanding distribution of its preys, here anchovy and sardine. However, this study pointed one drawback of the present modeling approach as potential spatial mismatches could occur in the future if the rate of climate change turns even faster (Durant et al., 2007).

4.2. Potential incidence of changes in small pelagic fish production on the food-web properties

The use of ENA indices in combination with the sensitivity analysis presented here allowed the characterization of emergent properties of the food web and the identification of potential changes in the overall flow organization pattern.

The D/H ratio showed an important decrease under the RCP 8.5 scenario that was not calculated for the intermediate scenario (RCP 4.5) despite the relatively highest detritivory highlighted by various flow values. The D/H ratio responded to the increase of particulate detritus export (less detrital matter available and associated flow values) and to the consequent lowering of detrital paths (both flows from bacteria and detritus; Table 2), suggesting a shift from a detritivorous functioning under present conditions and moderate climate change scenario (RCP 4.5) (Lassalle et al., 2011; Chaalali et al., 2015) to an herbivorous functioning. In addition, the ecological interpretation of the D/H ratio in relation with pressures and ecosystem stress remains controversial (Ulanowicz, 1992; Dame and Christian, 2007; Niquil et al., 2014b).

The ecosystem total activity (T..) augmentation predicted for the end of the century (RCPs 4.5 and 8.5) seemed in accordance with the rise in small pelagic fish production and with the exhaustive literature dedicated to the metabolic changes in relation with temperature (e.g. Arrhenius, 1889; Brown et al., 2004). However, given the stable A_i/C_i values, the internal organization of the ecosystem appeared to remain at a similar level not responding to a change in key compartment production. Moreover, the value of this index suggested that the major part of the ecosystem was not strongly organized. This non-organized part that corresponds to the redundancy (i.e. parallel trophic pathways) constitutes the reserves of the ecosystem and brings flexibility to the system by permitting its reorganization in case of disturbance (Ulanowicz, 2009). The redundancy can also be associated to the system omnivory (i.e. SOI index; Williams and Martinez, 2004 in Saint-Béat et al., 2015). Here, SOI showed close values whatever the environmental conditions, meaning that the variance of the prey trophic levels (for consumers) remained constant. This SOI index is often considered as a possible indicator of anthropogenic pressure (Lobry et al., 2008; Selleslagh et al., 2012). Nevertheless, this interpretation has to be nuanced. Despite the fact that omnivory may play an important role in the stabilization of food webs in response to a perturbation (see McCann and Hastings, 1997 in Saint-Béat et al., 2015), it does not have the same attenuation effect in all systems, depending on the trophic levels altered by the perturbation (Vandermeer, 2006 in Saint-Béat et al., 2015). Allesina et al. (2009) also suggested that the SOI index may only relate to redundancy with no consequences for the food-web or ecosystem robustness to a given pressure.

The cycling tended to increase in the intermediate scenario and even more in the “business-as-usual” scenario. This fact *a priori* seemed in contradiction with the decrease in the bacterial activity and the fall of detritivory observed under the RCP 8.5 scenario. This observation can be mainly explained by the increase in values of flows involved in the detritus-macrozooplankton-planktivorous pelagic fish-detritus loop. The higher cycling observed for the “business-as-usual” scenario suggested that, in relation to a reduction of detritus (higher exports outside the system), the system would compensate with a more efficient cycling processes. This observation is also in favor of a more dissipative system as first proposed by Baird et al. (1998). The higher cycling can be linked to the measure of the retention of carbon within the ecosystem as depicted by the APL values. Indeed, despite the higher export of detritus, the residency time of carbon was rising under climate change. According to Saint-Béat et al. (2015) that discussed the link between ecosystem resilience and cycling, and basing on De Angelis (1980), resilience could be linked to the time energy or matter stays within the system. Cycling increases the residence time of matter within the system (Herendeen, 1989 in Saint-Béat et al., 2015). Thus, the longer the residence time is, and the less resilient the system could be (De Angelis, 1980). Therefore, the increase in cycling could have a direct implication in terms of system resilience.

In conclusion, despite the methodological focus of the paper, all our results combined seemed to be in favor of a system adapting to sustain the increased production of small pelagic planktivores and comforting the view that this compartment could be assimilated to a 'biological pump' transporting carbon towards higher trophic levels in marine systems.

4.3. A methodology to assess "Good Environmental Status" (GES) in a context of climate change

The sensitivity analysis on small pelagics production led to ENA indices estimates with a higher variability under future climate scenarios. Despite the fact that the origin of the higher ENA variability could be, to some extent, imputable to the larger boundaries set for the small pelagics production, these results reinforced the observations made by a recent study (Niquil et al., submitted). Previous authors demonstrated that ENA indices were sensitive to a climatic shift in the Mediterranean Sea, affecting notably their variability. Also, the variance is often used as a mathematical tool to integrate climate-driven changes (Rodionov, 2004; Beaugrand, 2014; Beaugrand et al., 2015b).

As such, ENA indices constitute an interesting indicator integrating human-induced environmental changes into food-web properties (e.g. Tomczak et al., 2013; Luong et al., 2015; Schückel et al., 2015). This conclusion is promising in regards with EU evolving policy and decisions for ecosystem-based fisheries management. Thus, European directives expectations such as the Marine Strategy Framework Directive (MSFD) – which aims to assess the human activities impacts on the environment taking into account both the structure, function, and processes of marine ecosystems (EU, 2008), led to numerous studies on ecosystem health indicators (Borja et al., 2013; Piroddi et al., 2015). In the MSFD context, the OSPAR "COBAM - Food Webs expert group" proposed a list of nine indicators including ENA indices. Nevertheless, only fishery indicators [i.e. Large Fish Indicator (LFI) and Mean Trophic Level indicator (MTL)] are currently adopted as common indicators (Niquil et al., 2014a). The LFI, which is defined as the biomass of fish above a length threshold representing “large fish” expressed as a proportion of the total fish biomass (Greenstreet et al., 2011; Fung et al., 2012), is explicitly presented as a food-web indicator by the MSFD (EU, 2010). The MTL gives information on the structural changes in the ecosystem as a result of fishing and this impact could be generalized to the ecosystem level when using model-based MTL (Shannon et al., 2014). However, even if these two indicators describe some important features of the ecosystem and are presently tested in OSPAR regions, their scope is mainly focusing on benthic-demersal fish species and therefore not yet giving the “holistic” view recommended by the Food-Web COBAM expert group (Arroyo, pers. comm.).

The present work also emphasized the potential interest of considering ENA indices in addition to these actual common indicators (i.e. LFI and MTL) to describe marine food webs. More work still has to be done to gain insights on the joint effects of direct human pressures and climate change on ENA indices. For instance, this could be achieved by dedicating future modelling works to the alterations caused by climate and fisheries on the Bay of Biscay food-web functioning, as the two pressures are known to interact together (Perry et al., 2005; Planque et al., 2010).

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Table 1: Description of ENA indices used: names, abbreviations, and ecological interpretation.

ENA indices names	Codes	Equations	What does this index measure?
Total System Throughput	T..	Sum of all flows, i.e. consumption, respiration, imports and exports	the total quantity of carbon flowing within the ecosystem boundaries
Internal Ascendency	A_i	$\sum_{i=1}^{n}\sum_{j=1}^{n} T_{ij} \times log\left[\frac{T_{ij} \times T..}{\sum_{q=0}^{n+2} T_{qj} \sum_{v=0}^{n+2} T_{iv}}\right]$	nternal organization and activity of the ecosystem
Internal Capacity of Development	C_i	$-\sum_{i=1}^{n}\sum_{j=1}^{n} T_{ij} \times log\left[\frac{T_{ij}}{T..}\right]$	the maximal possible Internal Ascendency
Internal relative Ascendency	A_iC_i	$\frac{Ai}{Ci}$	state of internal organization (represents the organized part)
Average Path Length	APL	$\frac{TST}{\sum_i Exports + \sum_i Respiration}$	retention of carbon
Finn's Cycling Index	FCI	$\frac{TST_c}{TST} = \sum_j \frac{\sum_i T_{ij} + Imports_j}{TST}$	proportion of flows involved in loops (cycling)
System Omnivory Index	SOI	$\frac{\sum_i OI_i \times log[Q_i]}{\sum_i log[Q_i]}$	degree of feeding on several trophic levels
Detritivory/Herbivory ratio	D/H	Sum of flows originating from detritus and DOC compartments divided by the sum of flows from phytoplankton	easure of the relative importance of detritivory and herbivory activity in a given system

Table 2: Comparisons of flow mean estimates between the reference period 1994-2005 and the two RCP scenarios at the end of the century in 2090-2099 where '*' signifies that a difference is noticed (at least at the 70%-30% interval), whereas 'n.s.' signifies that no difference is noticed (i.e. the distributions were overlapping above the 65%-35% interval). '-' was used for a difference with a 65%-35% quantiles interval.

	Overlapping between $LIM\text{-}MCMC_{Ref}$ & $LIM\text{-}MCMC_{RCP\ 4.5}$			*Overlapping between* $LIM\text{-}MCMC_{Ref}$ & $LIM\text{-}MCMC_{RCP\ 8.5}$		
Flow description	**Interval 95%-5%**	**Interval 80%-20%**	**Interval 70%-30%**	**Interval 95%-5%**	**Interval 80%-20%**	**Interval 70%-30%**
Export of detritus	n.s.	n.s.	n.s.	n.s.	*	*
Detritus dissolution	n.s.	n.s.	n.s.	n.s.	n.s.	-
DOC Consumption by bacteria	n.s.	n.s.	n.s.	n.s.	n.s.	-
Production of DOC by bacteria	n.s.	n.s.	n.s.	n.s.	n.s.	*
Consumption of detritus by bacteria	n.s.	n.s.	*	n.s.	*	*

Figures captions

Figure 1: Study area of the Bay of Biscay continental shelf and locations of the main rivers flowing into it. The shaded area corresponds to the French part of the continental shelf (between 30- and 150-m isobaths), and represents the spatial extent of the LIM-MCMC.

Figure 2: Sketch diagram summarizing the methodological approach: **A.** Description of the combination of Ecological Niche Modeling, Linear Inverse Modeling, and Ecological Network Analysis. **B.** Description of the statistical comparison of flow and ENA indices values between the 3 situations (i.e. reference, RCP 4.5, and RCP 8.5). By generalizing this approach, an overlap at the 95%-5% quantiles interval was considered as 'significant', an overlap at the 80%-20% quantiles interval was considered as 'potentially significant', and both overlaps at the 70%-30% quantiles interval or at the largest quantiles interval 65%-35% were considered as 'trends'.

Figure 3: **A.** Mean (with associated standard deviation) of input flows for pelagic planktivorous fish and seabirds from the three LIM-MCMCs. White bars were for the reference period 1994-2005, grey ones for the RCP 4.5 2090-2099, and the black ones for the RCP 8.5 2090-2099. **B.** Mean of pelagic planktivorous fish consumption by seabirds (i.e. flow abbreviation pplTOsbr in Table S1) for the three LIM-MCMCs. The color code for the bars was the same as in the first panel.

The significance of the differences between the reference period and the future climate situations was given regarding the overlapping of the estimates distributions. An 'a' or 'b' code indicated if future scenario(s) differed from the reference period with additional'***' code for overlapping at the 95%-5% quantiles interval, '**' for overlapping at the 80%-20%

quantiles interval, ‘*’ for overlapping at the 70%-30% quantiles interval, and ‘.’ for overlapping at the largest quantiles interval 65%-35%.

Figure 4: Comparison of all the flow estimates concerning the macrozooplankton functional group for the three LIM-MCMCs. White bars are for the reference period 1994-2005, grey ones for the RCP 4.5 in 2090-2099, and the black for the RCP 8.5 in 2090-2099.

The significance of the differences between the reference period and the future climate situations was given regarding the overlapping of the estimates distributions. An ‘a’ or ‘b’ code indicated if future scenario(s) differed from the reference period with additional ‘***’ code for an overlapping at the 95%-5% quantiles interval, ‘**’ for an overlapping at the 80%-20% quantiles interval, ‘*’ for an overlapping at the 70%-30% quantiles interval, and ‘.’ for an overlapping at the largest quantiles interval 65%-35%.

Figure 5: **A.** Mean (with associated standard deviation) of input flows for planktonic functional groups get from the three LIM-MCMCs. White bars were for the reference period 1994-2005, grey ones for the RCP 4.5 in 2090-2099, and the black for the RCP 8.5 in 2090-2099. ‘maz’ was for macrozooplankton, ‘mez’ for mesozooplankton, ‘miz’ for microzooplankton, and ‘phy’ for phytoplankton. **B.** Mean (with associated standard deviation) of input flows for detrital and bacterial functional groups from the three LIM-MCMCs. White bars were for the reference period 1994-2005, grey ones for the RCP 4.5 in 2090-2099, and the black for the RCP 8.5 in 2090-2099. ‘bac’ was for bacteria, ‘det’ for particulate detritus, and ‘DOC’ for dissolved organic carbon.

The significance of the differences between the reference period and the future climate projections was given regarding the overlapping of the estimates distributions. An ‘a’ or ‘b’ code indicated if future scenario(s) differed from the reference period with additional ‘***’

code for an overlapping at the 95%-5% quantiles interval, '**' for an overlapping at the 80%-20% quantiles interval, '*' for an overlapping at the 70%-30% quantiles interval, and '.' for an overlapping at the largest quantiles interval 65%-35%.

Figure 6: Comparison of ENA indices' estimates for the three LIM-MCMCs. Triangle and diamond symbols were minimum and maximum estimates respectively. Dots were the mean ENA values estimated from one million simulations of the LIM-MCMC. Associated standard deviations were also shown. White, grey and black colors referred respectively to the reference period, the RCP 4.5, and the RCP 8.5.

The significance of the differences between the reference period and the future climate projections was given regarding the overlapping of the estimates distributions. An 'a' or 'b' code indicated if future scenario(s) differed from the reference period with additional '***' code for an overlapping at the 95%-5% quantiles interval, '**' for an overlapping at the 80%-20% quantiles interval, '*' for an overlapping at the 70%-30% quantiles interval, and '.' for an overlapping at the largest quantiles interval 65%-35%.

Figure 1

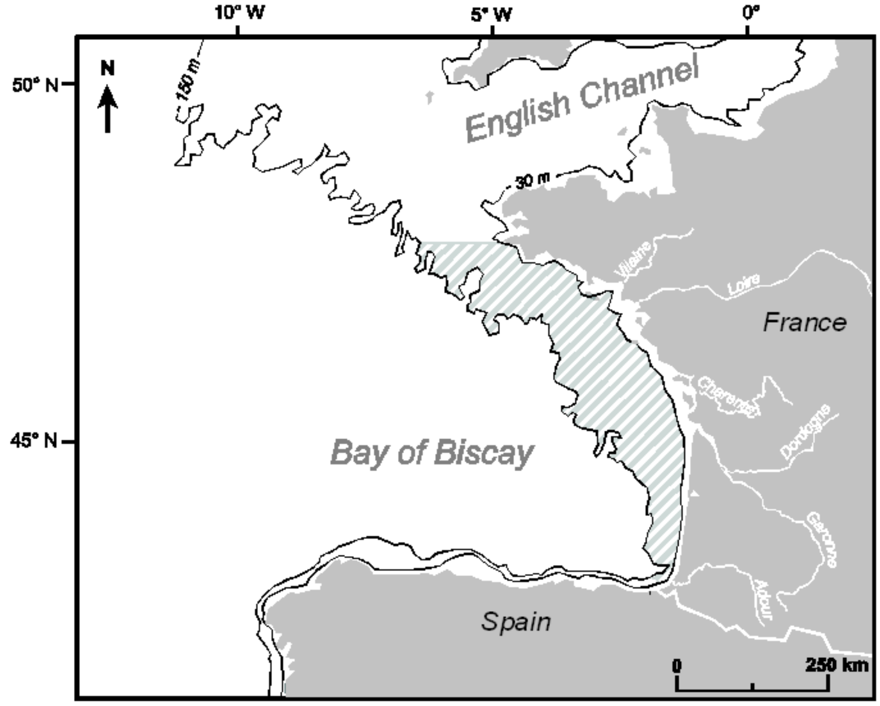
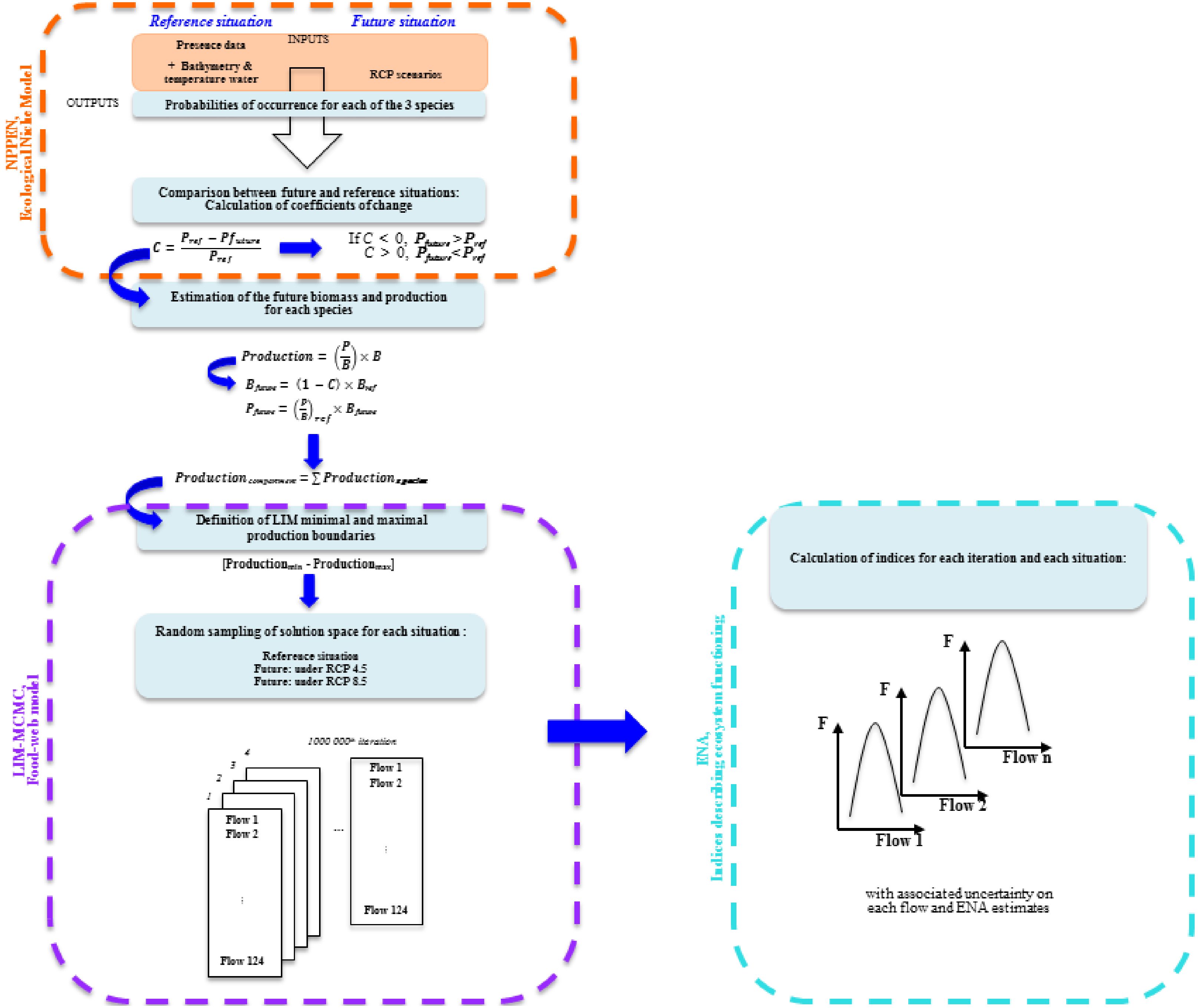
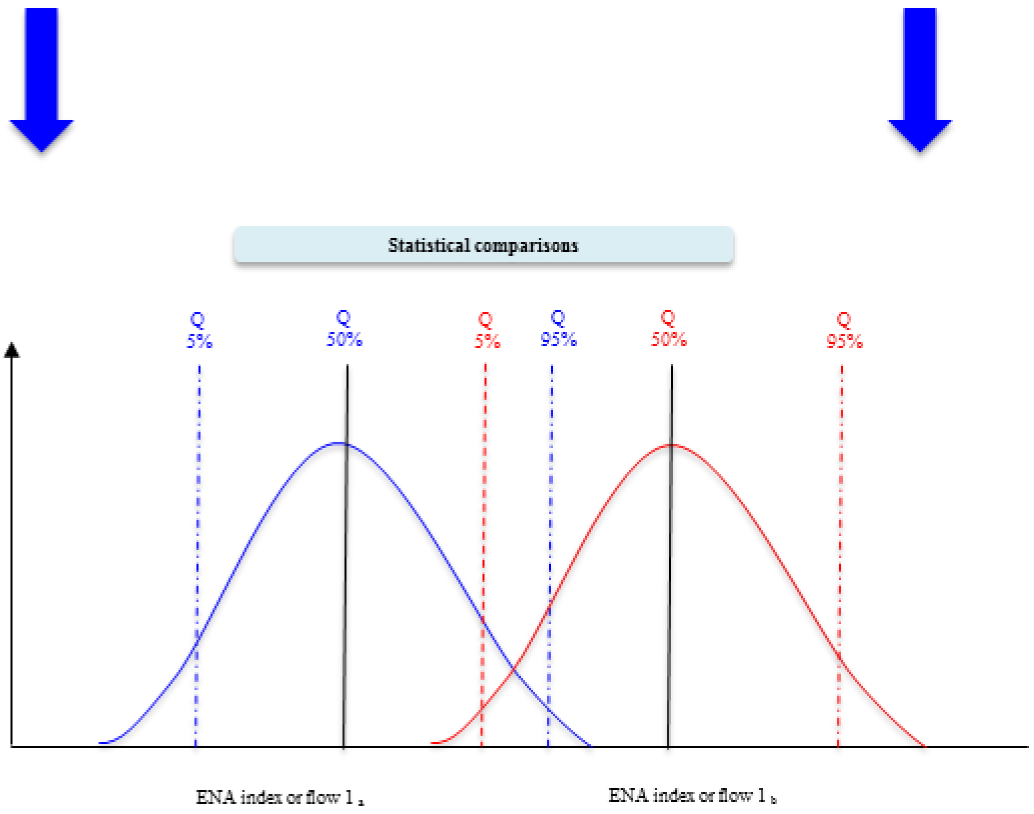

10° W
5° W
0°
50° N
45° N
N
150 m
30 m
English Channel
Vilaine
Loire
France
Charente
Dordogne
Garonne
Adour
Bay of Biscay
Spain
0
250 km

Figure 2

A


NPPEN,
Ecological Niche Model
Reference situation
Future situation
INPUTS
Presence data
+ Bathymetry & temperature water
RCP scenarios
OUTPUTS
Probabilities of occurrence for each of the 3 species
Comparison between future and reference situations:
Calculation of coefficients of change
$C = \frac{P_{ref} - Pf_{uture}}{P_{ref}}$
If $C < 0$, $P_{future} > P_{ref}$
$C > 0$, $P_{future} < P_{ref}$
Estimation of the future biomass and production for each species
$Production = \left(\frac{P}{B}\right) \times B$
$B_{future} = (1 - C) \times B_{ref}$
$P_{future} = \left(\frac{P}{B}\right)_{ref} \times B_{future}$
$Production_{compartment} = \sum Production_{species}$
LIM-MCMC,
Food-web model
Definition of LIM minimal and maximal production boundaries
$[Production_{min} - Production_{max}]$
Random sampling of solution space for each situation :
Reference situation
Future: under RCP 4.5
Future: under RCP 8.5
1000 000th iteration
1
2
3
4
Flow 1
Flow 2
Flow 124
...
Flow 1
Flow 2
Flow 124
ENA,
Indices describing ecosystem functioning
Calculation of indices for each iteration and each situation:
F
F
F
Flow 1
Flow 2
Flow n
with associated uncertainty on each flow and ENA estimates

B



Q 95%> Q 5% but no overlap at higher quantile intervals -> 'Significant' difference

Figure 3

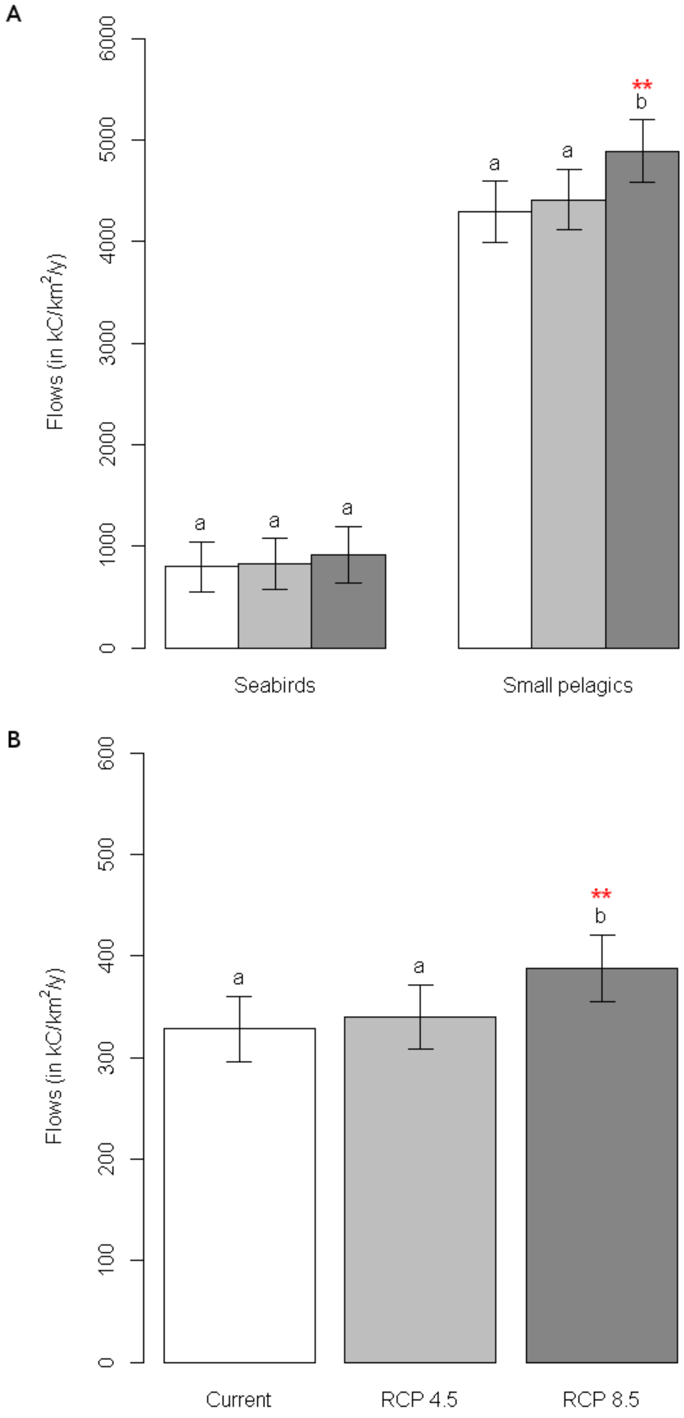
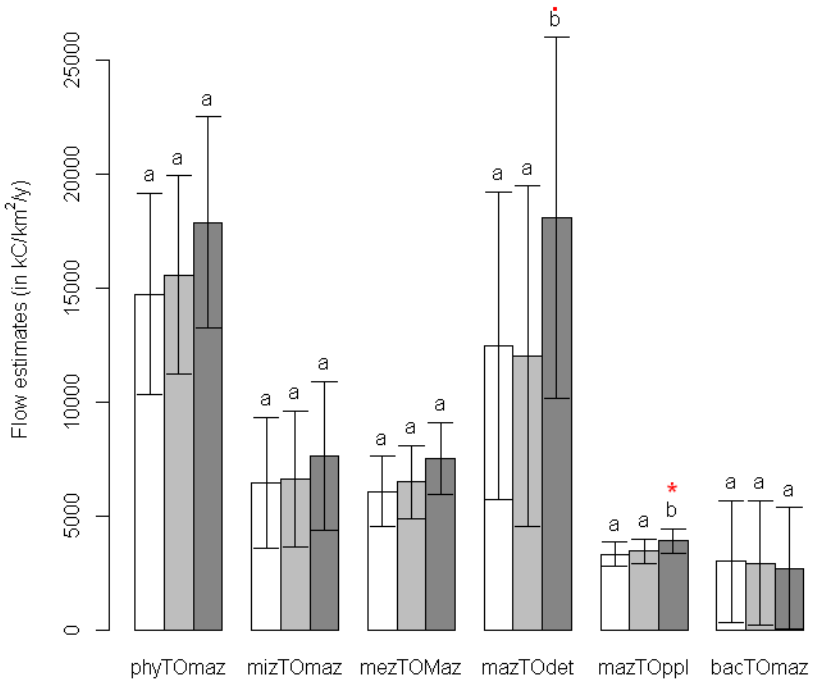

A
Flows (in kC/km^2/y)
0
1000
2000
3000
4000
5000
6000
a
a
a
a
a
**
b
Seabirds
Small pelagics
B
Flows (in kC/km^2/y)
0
100
200
300
400
500
600
a
a
**
b
Current
RCP 4.5
RCP 8.5

Figure 4


Flow estimates (in kC/km^2/y)
0
5000
10000
15000
20000
25000
a
a
a
a
a
a
a
a
a
a
a
b
*
a
a
b
*
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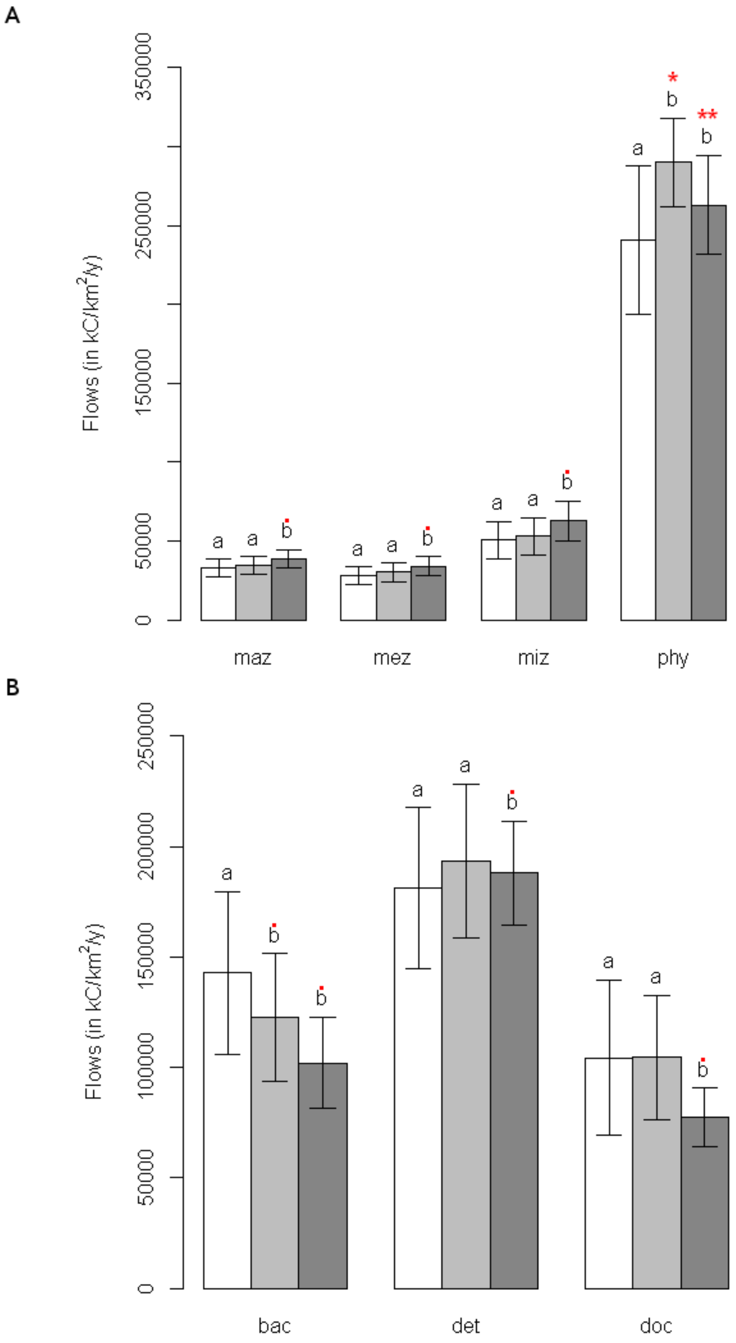
a
phyTOmaz
mizTOmaz
mezTOMaz
mazTOdet
mazTOppl
bacTOmaz

Figure 5


A
Flows (in kC/km^2/y)
0
50000
150000
250000
350000
a
a
b
a
a
b
a
a
b
a
*
b
**
b
maz
mez
miz
phy
B
Flows (in kC/km^2/y)
0
50000
100000
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a
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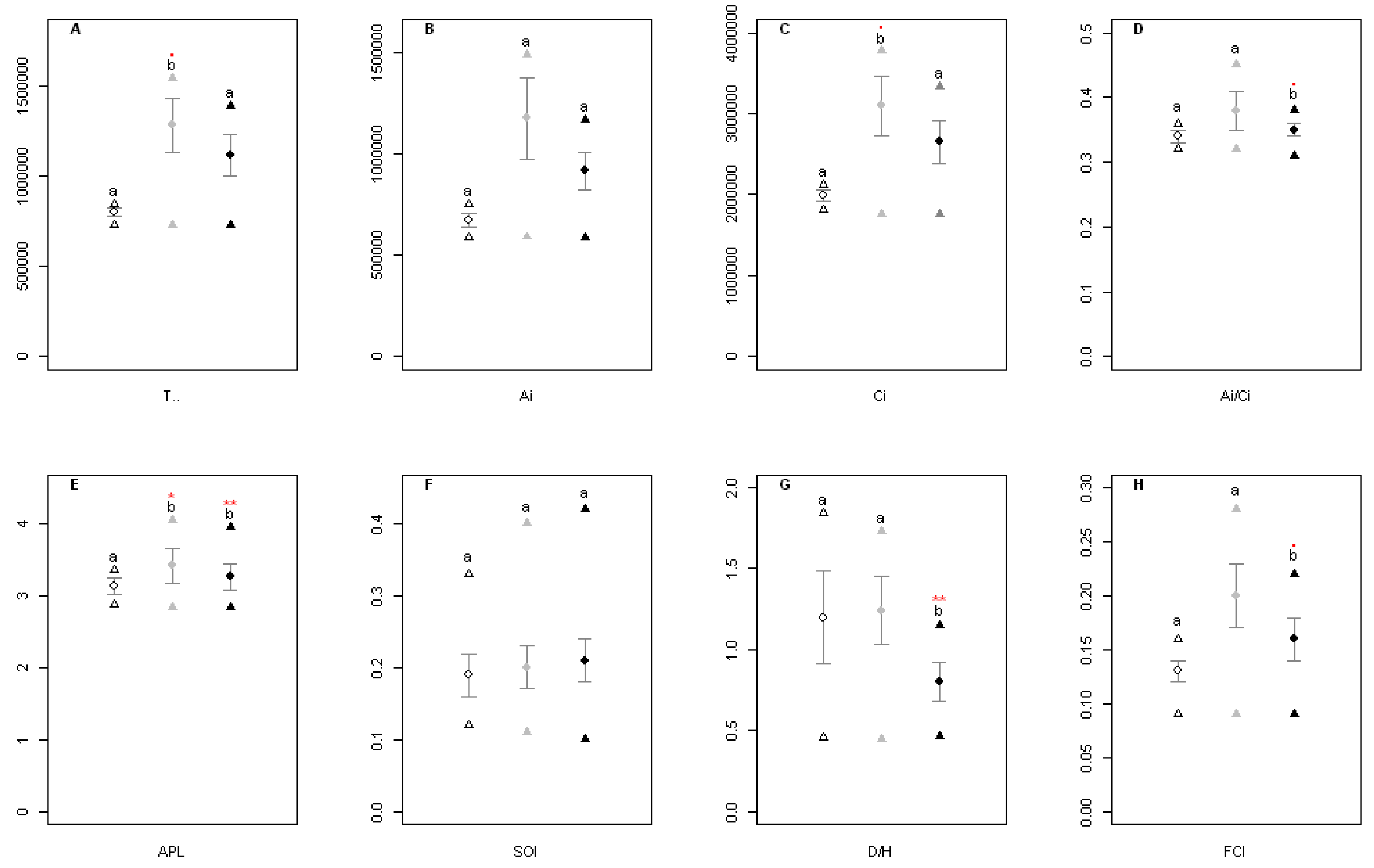
Figure 6


A
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C
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a
a
0
1000000
2000000
3000000
4000000
Ci
D
a
a
b
0.0
0.1
0.2
0.3
0.4
0.5
Ai/Ci
E
*
b
**
b
a
0
1
2
3
4
APL
F
a
a
a
0.0
0.1
0.2
0.3
0.4
SOI
G
a
a
**
b
0.0
0.5
1.0
1.5
2.0
D/H
H
a
b
a
0.00
0.05
0.10
0.15
0.20
0.25
0.30
FCI

References

Allesina, S., Bodini, A., Pascual, M., 2009. Functional links and robustness in foodwebs. *Philosophical transactions of the Royal Society: Biological sciences*, 364, 1701-1709.

Arrhenius, S., 1889. Über die Reaktionsgesechwindigkeit bei der Inversion von Rohrzucker durch Säure. *Journal of Research in Physical Chemistry*, 4, 226-248.

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., Gravel, D., 2013. From projected species distribution to food-web structure under climate change. *Global Change Biology*, 20(3), 730-741.

Alekseenko, E., Raybaud, V., Espinasse, B., Carlotti, F., Queguiner, B., Thouvenin, B., Garreau, P., Baklouti, M., 2014. Seasonal dynamics and stoichiometry of the planktonic community in the NW Mediterranean Sea: a 3D modeling approach. *Ocean Dynamics*, 64, 179-207.

Baird, D., Luczkovich, J., Christian, R.R., 1998. Assessment of spatial and temporal variability in ecosystem attributes of the St Marks national wildlife refuge, Apalachee Bay, Florida. *Estuarine, Coastal and Shelf Science*, 47, 329-349.

Baird, D., Asmus, H., Asmus, R., 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. *Marine Ecology Progress Series*, 462, 143−161.

Beaugrand, G., 2014. The effects of climate change on marine ecosystems. In: Seuront L. (eds.). Copepods : diversity, habitat and behavior. Nova Science Publishers.

Beaugrand, G., Luczak, C., Edwards, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology*, 15, 1790-1803.

Beaugrand, G., Lenoir, S., Ibanez, F., Manté, C., 2011. A new model to assess the probability of occurrence of a species, based on presence-only data. *Marine Ecology Progress Series*, 424, 175-190.

Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., Kirby, R.R., 2015a. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nature Climate Change*, 5, 695-701.

Beaugrand, G., Conversi, A., Chiba, S., Edwards, M., Fonda-Umani, S., Greene, C., Mantua, N., Otto, S.A., Reid, P.C., Stachura, M.M, Stemmann, L., Sugisaki, H., 2015b. Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Philosophical Transactions of the Royal Society B*, 370: 20130272. http://dx.doi.org/10.1098/rstb.2013.0272

Borja, A., Uriarte, A., Egana, J., Motos, L., Valencia, V., 1998. Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay (1967–1996). *Fisheries Oceanography*, 7, 375-380.

Borja, A., Elliott, M., Andersen, J.H., Cardoso, A.C., Carstensen, J., Ferreira, J.G., Heiskanen, A.S., Marques, J.C., Neto, J.M., Teixeira, H., 2013. Good Environmental Status of marine ecosystems: what is it and how do we know when we have attained it? *Marine Pollution Bulletin*, 76, 16-27.

Bopp L, Resplandy L, Orr JC, Doney, SC, Dunne, JP, Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., Vichi, M., 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, 10, 6225-6245.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecological Modelling*, 157, 281-300.

Braunisch, V., Suchant, R., 2010. Predicting species distributions based on incomplete survey data: the trade-off between precision and scale. *Ecography*, 33, 1–14

Brown, J.H., Gillooly J.H., Allen, A.P., Savage, V.M., West, G.B., 2004. Towards a metabolic theory of ecology, *Ecology*, 85, 1771-1789.

Casey, K.S., Brandon, T.B., Cornillon, P., Evans, R., 2010. The Past, Present and Future of the AVHRR Pathfinder SST Program, in Oceanography from Space: Revisited, eds. V. Barale, J.F.R. Gower, and L. Alberotanza, Springer, doi: 10.1007/978-90-481-8681-5

Chaalali, A., Beaugrand, G., Raybaud, V., Goberville, E., David, V., Boët, P., Sautour, B., 2013a. Climatic facilitation of the colonization of an Estuary by *Acartia tonsa*. *PLoS ONE,* 8(9): e74531.

Chaalali A., Chevillot X., Beaugrand G., David V., Luczak C., Boet P., Sottolichio A., Sautour B., 2013b. Changes in the zooplankton community distribution in the Gironde estuary: A marinisation consequence? *Estuarine, Coastal and Shelf Science,* 134, 150-161.

Chaalali, A., Saint-Béat, B., Lassalle, G., Le Loc'h, F., Tecchio, S., Safi, G., Savenkoff, C., Lobry, N., Niquil, N., 2015. A new modeling approach to define marine ecosystems food-web status with uncertainty assessment. *Progress in Oceanography*, 135, 37-47

Chust, G., Allen, J.I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M., Cannaby, H., Dadou, I., Daewel, U., Wakelin, S.L., Machu, E., Pushpadas, D., Butenschon, M., Artioli, Y., Petihakis, G., Smith, C., Garçon, V., Goubanova, K., Le Vu, B., Fach, B.A., Salihoglu, B., Clementi, E., Irigoien, X., 2014. Biomass changes and trophic amplification of plankton in a warmer ocean. *Global Change Biology*, 20, 2124–2139.

Dame, J.K., Christian, R.R., 2007. A statistical test of network analysis: Can it detect differences in food web properties? *Ecosystems*, 10, 906-923.

De Angelis, D.L., 1980. Energy flow, nutrient cycling, and ecosystem resilience. *Ecology,* 61, 764-771.

Doney, S.C., Sailley, S.F., 2013. When an ecological regime shift is really just stochastic noise. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 2438-2439.

Durant, J.M., Hjermann, D.O., Ottersen, G, Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33, 271-283

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430, 881-884.

EU, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Union,* L 164/19.

EU, 2010. Decision 2010/477/EU. Commision Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters. *Official Journal of the European Union*, L 232/14.

Farber, O., Kadmon, R., 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. *Ecological Modelling*, 160,115-130.

Finn, J.T., 1980. Plow analysis of models of the Hubbard Brook ecosystem. *Ecology,* 61, 562-571.

Frederiksen, M., Anker-Nilssen, T., Beaugrand, G., Wanless, S., 2013. Climate, copepods and seabirds in the boreal Northeast Atlantic–current state and future outlook. *Global Change Biology,* 19(2), 364–372.

Fung, T., Farnsworth, K.D., Reid, D.G., Rossberg, A.G., 2012. Recent data suggest no further recovery in North Sea Large Fish Indicator. *ICES journal of Marine Science*, 69, 235-239.

Goberville, E., Beaugrand, G., Hautkèete, N.-C., Piquot, Y., Luczak, C., 2015. Uncertainties in the projection of species distributions related to general circulation models. *Ecology and Evolution*, 5(5), 1100-1116.

Greenstreet, S.P.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E.J., Fraser, H.M., Fryer, R.J., 2011. Development of the EcoQO for the North Sea fish community. *ICES journal of Marine Science*, 68, 1-11.

Guesnet, V., Lassalle, G., Chaalali, A., Kearney, K., Saint-Béat, B., Karimi, B., Grami, B., Tecchio, S., Niquil, N., Lobry, J., 2015. Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. *Ecological Modelling*, 313: 29-40.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948-952.

Helaouët, P., Beaugrand, G., Edwards, M., 2013. Understanding Long-Term Changes in Species Abundance Using a Niche-Based Approach. *PLoS ONE*, 8(11): e79186.

Hermant, M., Lobry, J., Bonhommeau, S., Poulard, J.C., Le Pape, O., 2010. Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). *Journal of Sea Research*, 64, 45-53.

Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems*, 10(3), 488-502.

Hily, C., Le Loc'h, F., Grall, J., Glémarec, L., 2008. Soft bottom macrobenthic communities of the North Biscay revisited: a long term evolution under fisheries-climate forcing. *Estuarine, Coastal and Shelf Science*, 78, 413-425.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of the habitat suitability models to predict species presences. *Ecological Modelling*, 199, 142-152.

Hutchings, L., Barange, M., Bloomer, S., Boyd, A.J., Crawford, R.J.M., Huggett, J.A., Kerstan, M., Korrûbel, J.L., de Oliveira, J.A.A., Painting, S.J., Richardson, A.J., Shannon, L. J., Schülein, F.H., van der Lingen, C.D., Verheye, H.M., 1998. Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. *South African Journal of Marine Science*, 19, 211-225.

Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology*, 22, 415-427.

ICES, 2005. Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy (WGMHSA).

Irigoien, X., Fernandes, J.A., Grosjean, P., Denis, K., Albaina, A., Santos, M., 2009. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. *Journal of Plankton Research*, 31, 1-17.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J., Mavuti, K., 2006. Gaining insight into food webs reconstructed by the inverse method. *Journal of Marine Systems*, 60, 153-166.

Knutti, R., Sedlacek, J., 2012. Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, 3, 369-373.

Lampert, L., 2001. Dynamique saisonnière et variabilité pigmentaire des populations phytoplanctoniques dans l'Atlantique Nord (Golfe de Gascogne). Thèse de Doctorat en Oceanologie biologique, Université de Bretagne Occidentale, Brest, France.

Lassalle, J., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily, C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil, N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. *Progress in Oceanography*, 91, 561-575.

Latham, L.G., 2006. Network flow analysis algorithms. *Ecological Modelling*, 192, 586-600.

Lenoir, S., 2011. Impact du réchauffement climatique sur la distribution spatiale des ressources halieutiques le long du littoral français : observations et scénarios. Thèse de Doctorat, Université Lille 1, Lille, France.

Lenoir, S., Beaugrand, G., 2008. A climatic atlas of North Atlantic marine resources with a special emphasis on the English Channel and the North Sea. *Technical Report.* Centre

National de la Recherche Scientifique. Station Marine de Wimereux. Université des Sciences et Technologies de Lille 1. 515 p.

Lenoir, S., Beaugrand, G., Lécuyer, E., 2011. Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology*, 17, 115–129.

Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and stability of an estuarine trophic network. *Marine Ecology Progress Series*, 358, 13-25.

Luczak, C., Beaugrand, G., Jaffré, M., Lenoir, S., 2011. Climate change impact on Balearic shearwater through a trophic cascade. *Biology Letters*, 7(5), 702-705.

Luong, A.D., De Laender, F., Olsen, Y., Vadstein, F., Dewulf, J., Janssen, C.R., 2014. Inferring time-variable effects of nutrient enrichment on marine ecosystems using inverse modelling and ecological network analysis. *Science of the Total Environment*, 493, 708-718

Magnuson, J.J., Crowder, L.B., Medvick, P.A., 1979. Temperature as an ecological resource. *American Zoologist*, 19, 331-343.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P., Wilbanks, T.J., 2010. The next generation of scenarios for climate change research and assessment. *Nature*, 463, 747-756.

Niquil, N., Saint-Béat, B., Johnson, G.A., Soetaert, K., van Oevelen, D., Bacher, C.,Vézina, A.F., 2012. Inverse modeling in modern ecology and application to coastal ecosystems. *Treatise on Estuarine and Coastal Science*, Vol. 9 (pp. 115-133): Waltham: Academic Press.

Niquil, N., Baeta, A., Marques, J.C., Chaalali, A., Lobry, J., Patrício, J., 2014a. How does an estuarine food web react to disturbances? Lindeman's perspective. *Marine Ecology Progress Series*, 512, 141-154.

Niquil, N., Le Loc'h, F., Tecchio, S., Chaalali, A., Vouriot, P., Mialet, B., Fizzala, X., Féral, J.-P., Lamare S., Dauvin J.-C., Safi, G., 2014b. Trans-*Channel Forum Proceedings, Science and Governance of the Channel Marine Ecosystem*, 14 -15.

Niquil, N., Astorg, L., Tecchio, S., Chaalali, A., Safi, G., Raoux, A., Patricio, J., Lynam, C., Heymans, J.J., Tomczak, M.T., Hattab, T., Le Loc'h, F., Piroddi, C., Submitted. Shifting states of a Mediterranean food web evidenced by ecological network analysis. *Progress in Oceanography*.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annual *Review of Ecology, Evolution, and* Systematics, 37, 637-69.

Parmesan, C., Yohe, G., 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2004. Ascendency as ecological indicator: A case study on estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science*, 60, 23-35.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science*, 308, 1912-1915.

Petitgas, P., Alheit, J., Peck, M.A., Raab, K., Irigoien, X., Huret, M., van der Kooij, J., Pohlmann, T., Wagner, C., Zarraonaindia, I., Dickey-Collas, M. 2012. Anchovy population expansion in the North Sea. *Marine Ecology-progress Series*, 444, 1-13.

Piroddi, C., Teixeira, H., Lynam, C.P., Smith, C., Alvarez, M.C., Mazik, K., Andonegi, E., Churilova, T., Tedesco, L., Chifflet, M., Chust, G., Galparsoro, I., Garcia, A.C., Kämäri, M., Kryvenko, O., Lassalle, G., Neville, S., Niquil, N., Papadopoulou, N., Rossberg, A.G., Suslin, V., Uyarra, M.C., 2015. Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive. *Ecological Indicators*, 58, 175–191.

Planque, B., Lazure, P., Jegou, A.M., 2004. Detecting hydrological landscapes over the Bay of Biscay continental shelf in spring. *Climate Research*, 28, 41-52.

Planque, B., Fromentin, J.M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., Kifani, S., 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79, 403–417.

Quéro, J.C., Du Buit, M.H., Vayne, J.J., 1998. The records of tropical fishes and the warming of the European Atlantic waters. *Oceanologica Acta*, 21, 345-351.

Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M., Davoult, D., Morin P., Gevaert, F., 2013. Decline in kelp in west Europe and climate. *Plos One*, 8, e66044.

Raybaud, V., Beaugrand, G., Dewarumez, J.M., Luczak, C., 2015. Climate-induced range shifts of the American jackknife clam *Ensis directus* in Europe. *Biological invasions*, 17, 725-741.

Raybaud, V., Bacha, M., Amara, R., Beaugrand, G., Submitted. Climate-induced changes in the geographical range of the European anchovy (*Engraulis encrasicolus*), *Climatic change.*

Rochet, M.J., Daurès, F., Trenkel, V.M., 2012. Capacity management, not stock status or economics, drives fleet dynamics in the Bay of Biscay ecosystem on a decadal time scale. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 695-710.

Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters*, 31, L09204.

Saint-Béat, B., Dan, B., Asmus, H., Asmus, R., Bacher, C., Pacella, S.R., Johnson, G.A., David, V., Vezina, A.F., Niquil, N., 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological Indicators*, 52, 458-471.

Saint-Béat, B., Chaalali, A., Bopp, L., Lassalle, G., Beaugrand, G., Raybaud, V., Tecchio, S., Safi, G., Le Loc'h, F., Lobry, J., Niquil, N., In preparation. Consequences of climate changes on primary production and the overall food-web functioning of a marine ecosystem. *Progress in Oceanography.*

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature*, 413, 591-596.

Scheffer, M., Carpenter, S., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, 18, 648-656.

Schückel, U., Kröncke, I., Baird, D., 2015. Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. *Marine Ecology Progress Series*, 536, 25-38.

Selleslagh, J., Lobry, J., N'Zigou, A.R., Bachelet, G., Blanchet, H., Chaalali, A., Sautour, B., Boet, P., 2012. Seasonal succession of estuarine fish, shrimps, macrozoobenthos and plankton: Physico-chemical and trophic influence. The Gironde estuary as a case study. *Estuarine, Coastal and Shelf Science*, 112, 243-254.

Shannon, L., Coll, M., Bundy, A., Gascuel, D., Heymans, J.J., Kleisner, K., Lynam, C.P., Piroddi, C., Tam, J., Travers-Trolet, M., Shin, Y., 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series*, 512, 115-140.

Smith, W.H.F., Sandwell, D.T., 1997. Global seafloor topography from satellite altimetry and ship depth soundings: evidence for stochastic reheating of the oceanic lithosphere, *Science*, 277, 1956-1962.

Stebbing, A.R.D., Turk, S.M.T., Wheeler, A., Clark, K.R., 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *Journal of the Marine Biological Association of the United Kingdom*, 82, 177-180.

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experimental design. *Bulletin of the American Meteorological Society*, 93, 485-498.

Tomczak, M.T., Heymans, J.J., Yletyinen, J., Niiranen, S., Otto, S.A., Blenckner, T., 2013. Ecological network indicators of ecosystem status and change in the Baltic Sea. *Plos One,* 8(10), e75439.

Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. *Journal of Theoretical Biology*, 85, 223-245.

Ulanowicz, R.E., 1986. Growth & development: Ecosystems Phenomenology. Springer-Verlag, New York.

Ulanowicz, R.E., 1992. Ecosystem Health. In: R. Costanza, B.G. Norton, Haskell B.D. (eds.) Ecosystem health: New goals for environmental management, Island Press, Washington, DC, 190-225.

Ulanowicz, R.E., 2009. The dual nature of ecosystem dynamics. *Ecological Modelling*, 220, 1886-1892.

Ulanowicz, R.E., Abarca-Arenas, L.G., 1997. An informational synthesis of ecosystem structure and function. *Ecological Modelling*, 95, 1-10.

Varela, M., 1996. Phytoplankton ecology in the Bay of Biscay. *Scientia Marina*, 60, 45-53.

Van den Meersche, K., Soetaert, K., Van Oevelen, D., 2009. xsample(): an R function for sampling linear inverse problems. *Journal of Statistical Software*, 30, 1-15.

Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal* Society B, 365(1549), 2093-2106.