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Spatialized ecological network analysis for ecosystem-based management: effects of climate change, marine renewable energy, and fishing on ecosystem functioning in the Bay of Seine

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Abstract :

Integrative and spatialized tools for studying the effects of a wide variety of ecosystem drivers are needed to implement ecosystem-based management and marine spatial planning. We developed a tool for analyzing the direct and indirect effects of anthropic activities on the structure and functioning of coastal and marine ecosystems. Using innovative modelling techniques, we ran a spatially explicit model to carry out an ecological network analysis (ENA) of the effects of climate change (CC), of an offshore wind farm (OWF) and of multiple fishing scenarios on the Bay of Seine (eastern part of the English Channel) ecosystem. ENA indices described the effects of those different drivers in a holistic and spatial way. The spatial analysis of ecosystem properties revealed local and global patterns of modifications attributed to CC, while the OWF resulted in localized changes in the ecosystem. This ability of ENA indicators to detect human-induced changes in ecosystem functioning at various spatial scales allows for a more integrative view of the effects of human activities on ecosystems. ENA indices could be used to link both local and global ecosystem changes, for a more cross-scale approach to ecosystem management.

Highlights

►Ecological network analysis describes the spatial effects of multiple environmental drivers on the functioning of the extended Bay of Seine ecosystem. ►Climate change effect on species distribution had strong structuring effects on the ecosystem. ►A total of two fishing scenarios linked to Brexit (increased and decreased fishing) were tested; they had limited effects on ecosystem functioning compared to the effects of climate change on species distribution. ►Ecological network analysis distinguished vulnerable areas that might require special attention in terms of ecological management.

Keywords : climate change, ENA, ecological network analysis, Ecospace, ecosystem functioning, fishing effects, offshore wind farm, species distribution, trophic structure.

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1 Introduction

Marine ecosystems are crucial for human societies because they provide many services such as food provisioning, nutrient regulation, habitat maintenance and climate mitigation (Peterson and Lubchenco, 1997). Marine ecosystems are subject to pressures from human activities (Halpern *et al.*, 2008) and their subsequent detrimental impacts. Anthropogenic pressure is predicted to keep on increasing in the next decades due to the growing human needs (MEA *et al.*, 2005). This is reflected in the expanding number of offshore wind farms (OWFs) to meet the need for greener energy. The environmental impacts of OWFs occur in three phases: i) during the construction phase impacts may be considered temporary, the same can be said of the ii) decommission phase while iii) during the operational phase impacts are longer lasting (Petersen and Malm, 2006). The most significant long-lasting impacts of the operational phase on the whole ecosystem functioning include the reef effect caused by the turbine structures and the reserve effect resulting from fishing closure (Raoux *et al.*, 2019; Degraer *et al.*, 2020). Direct anthropogenic activities are not the only driver of ecosystems: climate change (CC) may also have many hard to predict effects (Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al*., 2016; Winder and Sommer, 2012a). These effects include (among others) drifts in species distribution (Cheung *et al*., 2009) and changing physiological rates (Brierley and Kingsford, 2009). Ecosystems are complex and interconnected. Unpredictable effects on several of their components could cascade through trophic chains and interactions, limit their resilience and thus facilitate regime shifts and ecosystem collapses (Levin and Lubchenco, 2008). In this situation, there is a growing need for integrative approaches to understand the sensitivity of such ecosystems to a wide variety of drivers.

The scientific community and the decision makers encourage the use of integrative approaches that can address an increasing complexity (Rombouts *et al.*, 2013) and number of anthropogenic pressures (de Jonge, 2007; Fath *et al*., 2019; Rodriguez, 2017). Integrative approaches are holistic methods employed to understand the functioning of whole ecosystems. Integrative or ecosystem-based approaches are considered essential for adequate ecosystem-based management (Agardy *et al*., 2011; Borja *et al*., 2010; Buhl-Mortensen *et al*., 2017) and have been highly advocated for sustainable management of marine and coastal environments (Langlet and Rayfuse, 2018).

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Ecological network analysis (ENA) is promising because it is compatible with ecosystem-based management and offers a quantitative assessment of marine ecosystem functioning (Niquil *et al.*, 2014a; Safi *et al.*, 2019; Heymans *et al.*, 2020). ENAs depict the ecosystem as a network of interactions, where information can cascade from one part of the network to the other. Derived from different sciences including economics and thermodynamics (Wulff *et al.*, 1989), ENA indices can quantify emerging properties of ecosystems and monitor their evolution (Ulanowicz, 1986; Heymans and Tomczak, 2016; Borrett and Scharler, 2019). Using ENA to spatialize ecosystem models would make them more operational and help marine spatial planning (Le Tissier, 2020).

Ecospace is a well-known spatio-temporal trophic model derived from the Ecopath with Ecosim framework (Walters *et al.*, 1999; Christensen and Walters, 2004). It can help marine spatial planning initiatives by simulating the effects of environmental changes on food webs (e.g. Alexander *et al.*, 2016; Liquete *et al.*, 2016). However, to our knowledge, no study has tested ENA in an Ecospace model. Combining ENA with Ecospace could give us a holistic view of the ecosystem under multiple schemes of environmental changes in order to link ecosystem-based management to marine spatial planning.

In this study, we propose to investigate the spatial effects of multiple drivers on the Bay of Seine (eastern part of the English Channel) ecosystem, using ENA indices. This work is based on the Ecospace model of Halouani *et al*. (2020) modified by Bourdaud *et al*. (2021). It represents the food web of the extended Bay of Seine (eBoS), and initially modeled the potential reserve effect of the future offshore wind farm (OWF) of Courseulles-sur-Mer (Halouani *et al*. 2020). It was also used to explore the potential effects of CC on species distribution (Bourdaud *et al*. 2021) by combining it with niche models (Ben Rais Lasram *et al.*, 2020).

Following these works, we integrated new approaches aimed at better forecasting the possible evolution of the Bay of Seine ecosystem. First, we added the reef effect to the potential impacts of the future OWF of Courseulles-sur-Mer. Secondly, we used the spatial-temporal framework module of *EwE* (Steenbeek *et al.*, 2013) to better model the likely effect of CC on species distribution in the Bay of Seine. Finally, we integrated fishing scenarios following the plausible effects of Brexit into the eBoS model. The spatial explanatory power

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of ENA indices was tested, both at a local scale inside the eBoS (OWF) and at a global scale across eBoS (CC and fishing scenarios), using these scenarios. We explored the spatial variability of the ecosystem properties and determined three functional regions with similar properties in the eBoS. We also discussed the sensitivity of the ecosystem properties to the different drivers within each functional region. By doing so, we determined the potential risk that such changes in ecosystem properties occur. We also highlighted the sensitive areas of the ecosystems that may require special attention from decision makers in the future, especially in the implementation of new OWFs in the English Channel. Finally, we investigated ENA sensitivity and explanatory power as a spatial planning tool.

2 Materials and methods

2.1 Study area

The extended Bay of Seine Ecospace model covers the sea space from the Cotentin peninsula to Le Havre all the way up to the French-British delimitation of the Exclusive Economic Zones (Figure - 1). It is a shallow coastal ecosystem open onto the English Channel, with a mean depth of 35 m varying from 5 m to around 70 m in the paleo-valley north-west of the eBoS. The eBoS covers 13,500 km²; the main sediment types include gravels, coarse sand, fine sand and muddy fine sand (Supplementary materials Figure S - 1 , Dauvin, 2015). Oceanographic features include the Seine estuary (south-east of the eBoS), and the Seine paleo valley (south-east to north-west of the eBoS) (Figure - 1). The Bay of Seine and the English Channel in general are a highly anthropized ecosystem, with numerous activities including fishing, aggregate extraction, marine renewable energy, tourism, sea freight and more (Dauvin, 2015). Fishing is very important in the bay, and more particularly king scallop (*Pecten maximus*) dredging, but many other fishing techniques are also used. Fishing gears include trawls and nets targeting demersal fish, trawls targeting small pelagic fish, demersal fish and cephalopods, as well as other fishing gears (Supplementary materials Table S - 1). The most harvested fish species include sole (*Solea solea*) and cod (*Gadus morhua*). The bay is also of great interest for renewable marine energy. The offshore wind farm of Courseulles-sur-Mer is under construction and should start operating in 2024 (~ 50 km², 64 turbines). Other offshore wind farm projects of various sizes are also under consideration in the bay.

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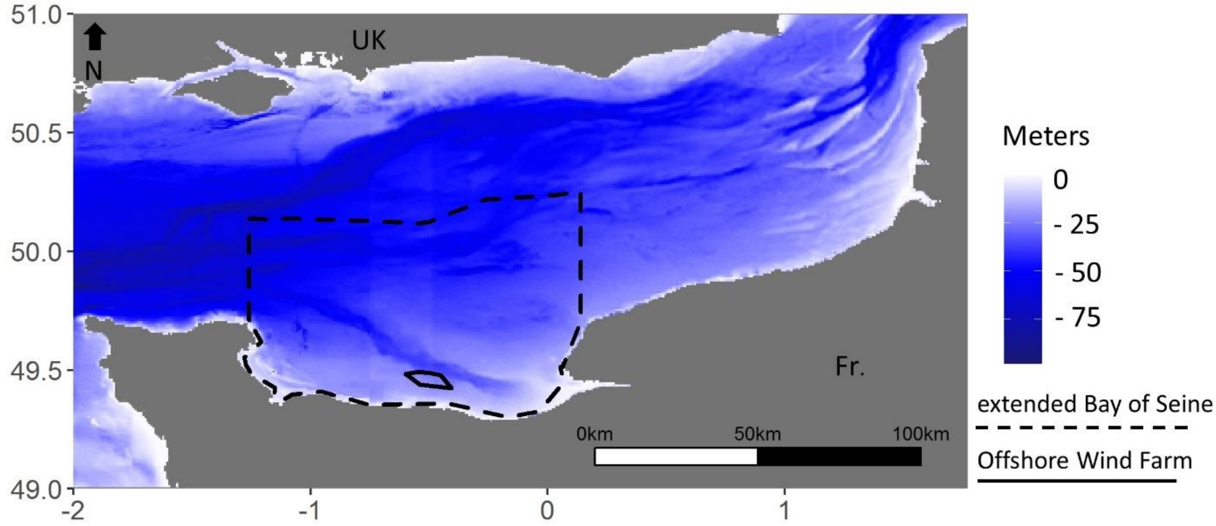

Figure - 1 Map of the eastern English Channel, including the boundaries of the extended Bay of Seine Ecospace model and the localization of the offshore wind farm of Courseulles-sur-Mer.

2.2 Food web modeling

The eBoS model was built from Ecopath with Ecosim (EwE 6) software. EwE can model marine food webs through a static average representation (Ecopath), with a time dynamics (Ecosim) and spatio-temporally (Ecospace).

The basic Ecopath model is a balanced model where the production of a trophic group is considered equal to its consumption by the system (Polovina, 1984; Pauly *et al.*, 2000). The production of each group of Ecopath follows the equation:

$$B_i.(P/B)_i = \sum B_j.(Q/B)_j.DC_{ij} + Y_i + E_i + BA_i + B_i.(P/B)_i.(1 - EE_i) \quad (1)$$

Where B is the biomass of prey i or predator j, $(P/B)_i$ is the production of i *per* unit of biomass, $(Q/B)_j$ is the consumption of j *per* unit of biomass, DC_{ij} is the fraction of i in the diet of j, Y_i is the total fishery catch rate of i, E_i is the net migration rate of i, BA_i is the biomass accumulation rate of i and EE_i is the ecotrophic efficiency of i or the proportion of i's production utilized in the system.

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The eBoS Ecopath model is composed of 40 living groups including a wide range of marine species – fish, invertebrates, birds and marine mammals – and 2 non-living groups – detritus and fishing discards. Living groups include monospecific groups as well as multi-specific groups (Supplementary materials Table S - 2). Multiple fishing techniques were modeled (trawling, nets, angling, traps, and other minor gears). A full description of the eBos model is available in *Halouani et al.* (2020).

Ecosim is a time-dynamic version of Ecopath and considers biomass variation over time (Walters *et al.*, 1997; Christensen and Walters, 2004). Ecosim represents the biomass dynamics as:

$$dB_j/dt = \frac{g_j.a_{ij}.v_{ij}.B_j.B_i}{2.v_{ij}+a_{ij}.B_j} - Z_j.B_j \qquad (2)$$

where B_j is predator j biomass, i the prey of j, g_j is the growth efficiency of j, v_{ij} is the prey vulnerability exchange rate, a_{ij} is the predator search rate, and Z_j is the total instantaneous mortality of j.

The eBoS Ecosim model was set to run from 2000 to 2015 and used 29 annual time series, including 21 time series of catches from the IFREMER database SACROIX (Système d'Information Halieutique, 2017) and 8 time series of biomass from multiple stock assessment campaigns. See Halouani *et al.* (2020) for more details.

Finally, Ecospace is a spatially explicit time-dynamic model based on Ecopath and Ecosim. In Ecospace, the spatial extent of the ecosystem is represented by a grid of cells and each cell is a time-dynamic trophic model based on Ecosim, with interconnections between cells (Walters *et al.*, 1999; Christensen *et al.*, 2014). The base map of the eBoS Ecospace model was made of 4,907 cells, with a resolution of 0.015°x 0.015° each, identified depending on their row r and their column c (r,c). Input maps included a bathymetric map to define the model area, extracted from GEBCO (General Bathymetric Chart of the Oceans: https://www.gebco.net/) and a map of primary production from SeaWifs representing the relative chlorophyll a concentration in the bay in 2000 (https://podaac.jpl.nasa.gov/). A habitat map was used to define species distributions in the initial model of Halouani *et al*. (2020), but it was replaced with niche model suitability index maps in Bourdaud *et al*. (2021)

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(Supplementary materials Table S - 3). These suitability index maps were computed using multi-algorithm niche models (Ben Rais Lasram *et al*., 2020, Supplementary materials Figure S - 2 to 28). Niche model algorithms are correlative approaches aimed at identifying the potential niches of species by correlating species occurrences with environmental variables. The niche models developed by Ben Rais Lasram *et al.* (2020) used presence-only data correlated with climatic variables (temperature and salinity) as well as habitat variables (type of substrate, depth, slope, and orientation). Eight models from BIOMOD were used. Model fit was determined using a 3-fold cross validation procedure and model performance was assessed using both the Continuous Boyce Index or CBI and the True Skill Statistic or TSS. Only the models with an averaged CBI superior to 0.5 were kept (Supplementary materials Table S 4 & 5). All the modeling choices can be found in Ben Rais Lasram *et al*. (2020). Averaged suitability index maps were then built from the fitted species distribution models, using climatic and habitat-based species distribution models, and were validated using expert knowledge.

Averaged suitability index maps were computed for 72 species of the eBoS and were employed as environmental driver maps for most of the groups of the Ecospace model (Coll *et al.*, 2019). Some groups considered poorly modeled by the niche models were driven by other parameters, e.g. depth (Supplementary materials Table S - 3). Monospecific niche model outputs were directly applied for monospecific trophic groups and merged according to the biomass of each species in multi-specific groups. The multi-specific trophic groups lacking data to model the distribution of all the species of the group were driven by the suitability index map of the dominant species of the group (Bourdaud *et al*., 2021).

Environmental drivers (h) were used to compute the habitat capacity (C_{rcj}) of each trophic group j in each cell (r,c) of the eBoS Ecospace model and define suitable habitats for each group of the model (Christensen *et al*., 2014). The habitat capacity drove the vulnerable prey densities (V_{ij}) as well as the vulnerability exchange rate (v_{ij}), the search rate (a_{ij}) and the predation rate (z_j) to set suitable environments for all the groups of the model according to their environmental preferences. Predators fed themselves according to their habitat capacity and based on prey availability. The prey pool available for each predator is fixed and

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defined in the Ecopath diet matrix. The habitat capacity C_{rcj} ranged between 0 and 1 and was calculated for each cell as a function of a vector of habitat attributes (environmental drivers):

$$C_{rcj} = f_j(h_{r,c}) \tag{3}$$

$$V_{ij} = \frac{v_{ij}.B_j}{2.v_{ij} + a_{ij}.\frac{B_j}{C_{rcj}}} \tag{4}$$

Where B_j is the biomass of predator j, v_{ij} is the vulnerability exchange rate, and a_{ij} the search rate.

Multiple types of environmental drivers can define the habitat capacity of a species (water depth, temperature, or suitability index maps from niche models, Supplementary materialsTable S - 3), and each environmental driver is associated with a specific response curve. In the eBoS model, a linear response curve was associated to the niche model results to compute the habitat capacity of each species (see De Mutsert *et al.*, 2017). The suitability index of the niche models varied between 0 (not suitable) and 1 (suitable), like the habitat capacity (Bourdaud *et al.*, 2021). Other response curves were built for the other groups (Supplementary materials Figure S - 29 to S - 34).

The eBoS model simulated multiple scenarios and each scenario modeled one driver. In the first scenario, we modeled the potential long-term effects of the future OWF of Courseulles-sur-Mer. The second and third scenarios modeled the likely effects of CC on species distribution in the bay of Seine under the RCP8.5 forcing scenario of the IPCC (Intergovernmental Panel on Climate Change) that appears to be the most realistic one (Schwalm *et al.*, 2020). Finally, we built two fishing scenarios linked to the potential effects of Brexit: a “reduced fishing activities” scenario – F_red – and an “increasing fishing activities” scenario – F_inc (Figure – 2).

ENA required working with a mass-balanced model. As such, we did not work in a temporal way and we only needed “snapshot” of trophic flows. Ecospace was used to create end maps of indices for each scenario (Figure – 2) at a mass-balanced state.

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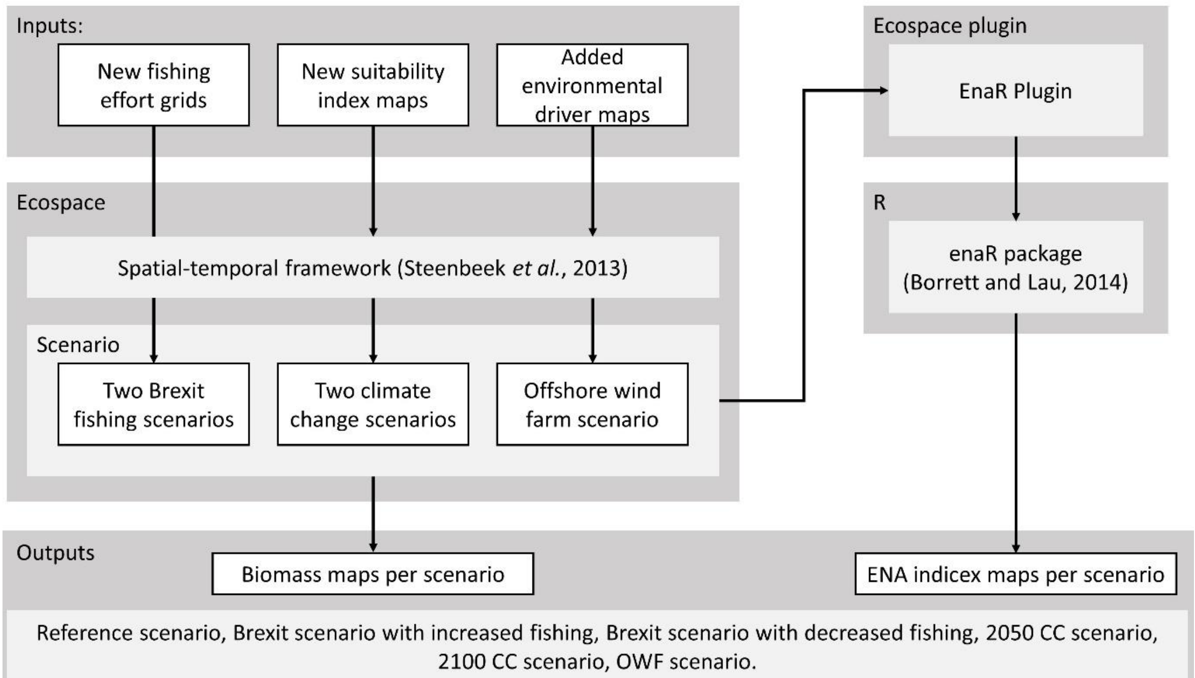

Figure – 2 Modeling framework. eBoS, extended Bay of Seine; ENA, ecological network analysis; OWF, offshore wind farm; CC, climate change.

2.3 Effect of climate change on species distribution

In Bourdaud *et al*. (2021), a first set of suitability index maps was computed using niche models with climate parameters over the 2005 – 2012 period (Ben Rais Lasram *et al.*, 2020). It was defined as the initial environmental driver for 27 of the 40 living groups, from benthic invertebrates to piscivorous fish (Supplementary materials Table S - 2). Groups were chosen based on data availability and distribution models results. To model the effect of CC on the distribution and dynamics of eBoS species, two new sets of suitability index maps were computed with niche models, using climate projections under the IPPC “business as usual” scenario RCP 8.5 (Ben Rais Lasram *et al.*, 2020), but at different time intervals: one in 2050 (2041 – 2050) and one in 2100 (2091 – 2100). Using these new niche models, we determined the evolution of the suitability index under the effects of climate change for the 27 living groups using environmental driver. This allowed us, to model the potential effect of climate change on a large part of the food web, from benthic invertebrates to piscivorous fish but not in its entirety.

The suitability index defined the theoretical niche of the species, between the realized niche and the fundamental one (Soberón and Nakamura, 2009; Jiménez *et al.*, 2019). Considering the fundamental niche as the extent of geoclimatic parameters where species

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have a positive production rate (Hutchinson, 1957), we hypothesized that the production of the species would be lower close to the limit of the theoretical niche (lower suitability index), and higher in the center of the theoretical niche (higher suitability index). The niche models simulated how suitable the geoclimatic parameters were and their evolution by 2050 and 2100, following the IPPC “business as usual” scenario RCP 8.5.

Like the Ecospace model outputs, the niche model outputs used to model the effects of climate change were all validated by experts (pers. Com. Jean-Claude Dauvin, Jean-Paul Robin and Éric Foucher), and the results were similar to those of other works on similar species in the English Channel (Rombouts *et al.*, 2013).

Averaged suitability index maps for each of the 27 groups were computed for the two climate change projections (2050 and 2100), and were introduced in Ecospace using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013) to model the effects of climate change. The spatial-temporal framework was used with the following protocol: all Ecospace scenarios were first started with the initial suitability index maps as environmental drivers computed from 2005 – 2012 climate parameters. After 20 years of spin-up used to reach stable biomass for each group, the suitability index maps of the CC niche models were introduced to replace the initial suitability index maps and to model the effect of CC on species distribution in the two CC scenarios. Subsequently, Ecospace scenarios were run until group biomass values were considered stable and reached a balanced state, as required by ENA. The models were run for 55 years after the spin-up in each CC scenario. The results retrieved after stabilization were used to compute ENA indices.

By replacing the initial suitability index computed from 2005 – 2012 climate parameters with suitability index sets computed from the effects of climate change on climate parameters, we modified the environmental driver for each of the 27 groups, to reflect the effects of climate change in 2050 and in 2100. The aim was to reflect the impact of climate change on the biogeoclimatic niches of the trophic groups: as climate change modifies the environment, geoclimatic parameters become more or less suitable for the species of the trophic groups and modify habitat suitability (see Coll *et al.*, 2019). Following the foraging arena theory, if the habitat becomes more or less suitable for a group (according to niche models), then the habitat capacity changes accordingly and modifies the group dynamic in Ecospace (Walters *et*

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al., 1999; Christensen *et al.*, 2014). If the suitability index of a group decreases between the reference niche model — computed from the 2005 – 2012 climatic parameters — and one of the climate change niche models — IPPC "business as usual" scenario RCP 8.5 —, the habitat capacity of the group is reduced (C_{rcj}). Consequently, the habitat is less suitable for the group j, consumption of I by j decreases (Christensen *et al.*, 2014; Coll *et al.*, 2019), and so does the production of j (Eq. 4). Therefore, the evolution of biomass distribution in the Ecospace model due to climate change depends both on the suitability index of the species (evolution of abiotic parameters) and on prey availability (biotic relationship between species), allowing for a more realistic simulation of the effects of climate change (see Bourdaud *et al.*, 2021).

Using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013), we produced end model results for the two CC time intervals rather than modeling the "continuous" impact of CC from the current period to the 2050 or 2100 horizon.

2.4 Fishing scenarios

To evaluate the significance of the effects of fishing on the ecosystem, we designed multiple fishing effort functions (Supplementary materials Table S – 6 to S - 8), to model the potential effects of Brexit on fishing effort in the eBoS (Walters *et al.*, 1999). Two new scenarios were built: one with a decreased fishing pressure (**F_dec**) and one with an increased fishing pressure (**F_inc**) compared to the reference scenario.

- **F_dec** considered a decrease of the fishing activities in the area. Such a decrease would be the result of the closing of British fishing areas to French fishermen. Those areas are considered very rich in fish resources (*https://atlas-transmanche.certic.unicaen.fr/en/*), so it was speculated that fishermen would lose part of their income and could decide to stop or shift their activity. As France provides strong support to European fishing, French fishermen could be helped find other jobs, and this would limit French fishing in the area. By looking at the "fishing vessel activity" report of Caen by the Ifremer (Ifremer SIH, 2017), we supposed that medium-sized to small ships (< 12 m) would be more impacted. Such vessels mainly performed 3 fishing activities in the eBoS model ("pelagic and bottom trawls", "bottom trawls", "pelagic trawls"), as well as "other fishing gears". To model the potential effects of this scenario, we approximated a 20% reduction of the "trawl" activities and a 5 %

reduction of "other fishing gears". Moreover, British fishermen would not be able to catch king scallops in French waters anymore, and in the absence of potential modifications of quotas, this would result in a lower fishing pressure in the area. The "dredge" gear activity would thus be reduced by 20 % based on British quotas on king scallops.

- **F_inc** considered an increase of fishing in the area resulting from the relocation of European fisheries from France, Belgium, The Netherlands or even Denmark inside the eBoS. As European fishermen would not have access to the United Kingdom waters, they would have to fish in other places, e.g. in the eBoS. King scallop fishing would still be reduced, as no new quotas are likely to be set to let other countries take up the UK's vacant place, even though some French fishermen could benefit from it. In our scenario, this resulted in a 20 % increase of the "pelagic and bottom trawls", the "bottom trawls" and the "pelagic trawls" activities, as well as a 5 % increase of "other fishing gears" activities based on the previous Brexit scenario.

Following the December 2020 negotiations between the European Union and the United Kingdom government, decisions on fishing have been postponed till 2026, making our scenarios still plausible to this day.

New fishing effort grids were built from the initial model of Halouani *et al*. (2020) and modified according to the desired scenario (Supplementary materials Table S – 6 to S - 8). Fishing effort in each fishing scenario was considered constant, because we only looked at the "end picture" of each scenario.

2.5 Offshore wind farm

Recently there has been an increasing interest to understand potential effects of OWFs on marine ecosystems (Shields and Payne, 2014). They have been split into three main categories depending on the phase of life of the offshore wind farm: 1, construction; 2, routine operation; 3, decommission (Gill, 2005; Shields and Payne, 2014). While the construction and decommission phases are characterized by a strong and abrupt impact on the ecosystem, the operating phase is characterized by a long and structuring effect lasting as long as the park is operating (Gill, 2005; Petersen and Malm, 2006; Wilhelmsson *et al.*, 2006; Wilhelmsson and

Malm, 2008). This study targets the two main structuring effects of the operating phase on the whole ecosystem: the reef effect and the reserve effect (Petersen and Malm, 2006; Raoux *et al.*, 2019; Degraer *et al.*, 2020). To model these impacts, we used tools available in Ecospace and data from a previous Ecopath model of the Courseulles-sur-Mer OWF (Raoux *et al*., 2017).

Spatial restrictions are likely to be implemented around offshore wind farm installations for navigation safety which could lead to a limitation of fishing activities: this is the above-mentioned reserve effect. Modeling the reserve effect induced by the OWF was straightforward and had previously been achieved by Halouani *et al.* (2020) using the MPA tool of Ecospace. To do so, multiple cells of the Ecospace model inside the future OWF were closed to fishing. Only 15 % of the OWF surface was blocked to all fishing activities so as to represent the OWF owners' proposal during the environmental impact assessment, to "optimize" the fishing area by leaving a sufficient space between turbines and connecting cables (Raoux *et al.*, 2018).

Due to the small footprint of the OWF foundation compared to the Ecospace cell resolution (5% of a single cell), modeling the reef effect was not possible by simply changing the habitats in the cells. We had to look at a previous model of the reef effect of the Courseulles-sur-Mer OWF (Raoux *et al*., 2017). The observations on this Ecopath model were linked to the 70 km² farm in Ecospace (37 cells). In Raoux *et al*. (2017), the reef effect was modeled by forcing the biomass of 10 trophic groups and the replacement of soft sediment by hard substrates was thus considered insignificant. We did the same by creating new environmental maps for the same groups in the eBoS Ecospace model to represent the biomass variations caused by the reef effect (Supplementary materials Table S - 9). The increased habitat suitability due to the reef effect would thus lead to a higher foraging capacity based on the foraging arenas theory (Walters *et al.*, 1997; Ahrens *et al.*, 2012). The new environmental maps were added using the spatial-temporal framework of Ecospace at the 2015 time step, before the CC simulations. Similar structural sub-regions were used to characterize the effects of the OWF on the eBoS ecosystem (Halouani *et al*. 2020): the OWF area itself, the first two rows of cells surrounding the farm (spillover 1), the next two rows of cells surrounding the farm (spillover 2) and the rest of the eBoS model (Bay) (Supplementary materials Figure S - 35).

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2.6 Ecological network analysis

Ecological network analysis indices are holistic indices describing the functioning and organization of the food web. They are computed from flow matrices of the food web. ENA indices were computed for each cell of the Ecospace model with a beta Ecospace plugin: "EnaR" (Table - 1). This plugin allows Ecospace to build SCOR files for each cell of the model at every time step. Based on the SCOR file, the ENA indices were calculated with the“"ena”" R package (Borrett and Lau, 2014). ENA indices were calculated for the 4,907 cells of the Ecospace model in the extended Bay of Seine. They were computed for the initial reference current scenario, for the two CC scenarios, for the two fishing scenarios and for the OWF scenario.

Table - 1 ENA indices computed with enaR from Ecospace SCOR files.

Name	Objective	Calculation	References
Relative redundancy of the flow (RDC)	The relative redundancy is the "reserve" of the system information and refers to the extent of parallel flows in the system relative to the total capacity of the system.	$\Phi_i = -\sum_{i,j=1}^{n} T_{ij}\log[\frac{T_{ij}^2}{T_i T_j'}]$ Where Φ_i is the internal relative redundancy, $T_{ij}$the flow between i and j, T_i the sum of all the flows leaving i, T_j' the sum of all the flows leaving j. $RDC = \frac{\Phi_i}{DC}$ Where DC is the development capacity of the system.	(Ulanowicz and Norden, 1990; Christensen, 1995; Ulanowicz *et al.*, 2009)
Total flow diversity (H)	Flow diversity quantifies the diversity of flows passing through all the groups of the model.	$H = \sum_i \sum_j f_{ij}\log(f_{ij}Q_i)$ Where f_{ij} is the fraction of the total flow from j that passes through I, and Q_i is the probability that a unit of energy passes through i.	(Christensen, 1995)
Mean trophic efficiency / Mean transfer Efficiency (TE)	The mean trophic efficiency describes the mean percentage of production of one trophic level converted to production by the next trophic level. It is averaged for the entire trophic network.	Using Lindeman spine, the trophic efficiency for a trophic level tl was computed as: $TE_{tl} = \frac{T_{.tl+1}}{T_{.tl}} \times 100$ Where $T_{.tl}$ is the total outflow for trophic level tl, and $T_{.tl+1}$ is the total outflow for the next trophic level. The 'mean trophic efficiency' of the system is then derived from the geometric	(Lindeman, 1942; Niquil *et al.*, 2014)

		mean of the efficiencies of all trophic levels.	
System omnivory index (SOI)	The system omnivory index quantifies the distribution of trophic interactions among different trophic levels. It is the mean omnivory index of all the groups.	$OI_i = \sum_{j=1}^{n} [TL_j - (TL_i - 1)]^2 \times DC_{ij}$ $SOI = \frac{\sum_{i=1}^{n} [\mathrm{OI}_i \times \log(Q_i)]}{\sum_{i=1}^{n} \log(Q_i)}$ where TL is the trophic level of i or j.	(Libralato, 2013)
Recycling index or Finn Cycling Index (FCI)	The recycling index is the fraction of energy recycled in the system.	$FCI = \frac{TST_c}{TST}$ where *TST* is the total system throughflow, and *TSTc* the cycled total system throughflow.	(Finn, 1980)
Mean trophic level (MTL2)	The MTL2 is the mean trophic level of the network's groups, taking all level-2 consumers into account.	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ where B is the biomass of i or j.	(Latham, 2006)

2.7 Statistical analysis

In order to better understand the effects of each scenario spatially, a K-means clustering analysis was carried out (MacQueen, 1967) on the ENA results of the current reference scenario. The "Elbow" method was used to determine the optimal value of the cluster based on multiple K values and their effects on the averaged distance between points (sum of the square).

A Cliff delta was used to test the significance of the differences between the ENA values of the reference scenario and those of the different scenarios modeling the effects of a driver. In previous works, the Cliff Delta (Cliff, 1993) proved useful to compare ENA results when large sample sizes and heteroscedasticity precluded the application of parametric statistical tests (Tecchio *et al.*, 2016; V. Girardin & J. Lequesne, pers. comm.). We employed the non-parametric Cliff Delta with the same threshold as Romano *et al*. (2006), who considered differences between datasets negligible if the Cliff Delta (| ∂Cliff |) was < 0.147, low if 0.147 < | ∂Cliff | < 0.33, medium if 0.33 < | ∂Cliff | < 0.474, or strong if | ∂Cliff | > 0.474.

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3 Results

3.1 Regionalization of the model

The ENA values of the reference scenario were higher near the coastline and especially near the Seine estuary south east of the eBoS model, for the 6 indices; they were lower in the deepest, most offshore part of the eBoS, north west of the eBoS model (Figure - 3). While most of the indices followed this trend, the FCI obviously differed, with a pattern closer to the primary production pattern (Supplementary materials Figure S - 36). Overall, this indicates that the flow diversity, the relative overhead, the mean trophic level and to a lesser extent recycling seemed to follow a coastline / open sea gradient.

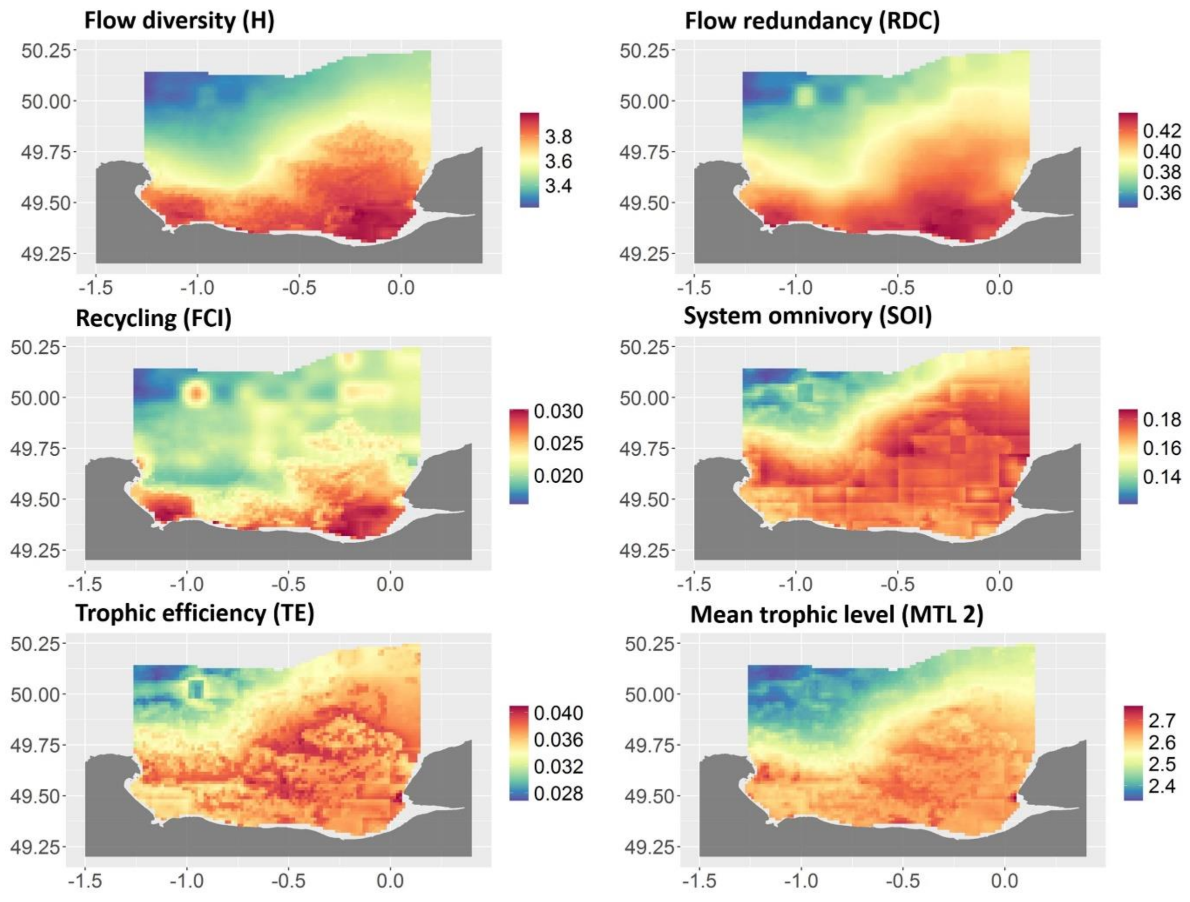

Figure - 3 Maps of ecological network analysis indices for the reference scenario.

The K-means clustering analysis associated to the “elbow” method determined three to four clusters. In order to simplify the analysis and because three clusters provided better spatial delimitation, we set it at three. The three clusters revealed a gradient from the

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coastline to the open sea (Figure - 4). The clusters were named accordingly, with the most coastal cluster called “Coastal Bay of Seine”, the following one “Offshore Bay of Seine” and the last one “Central English Channel”.

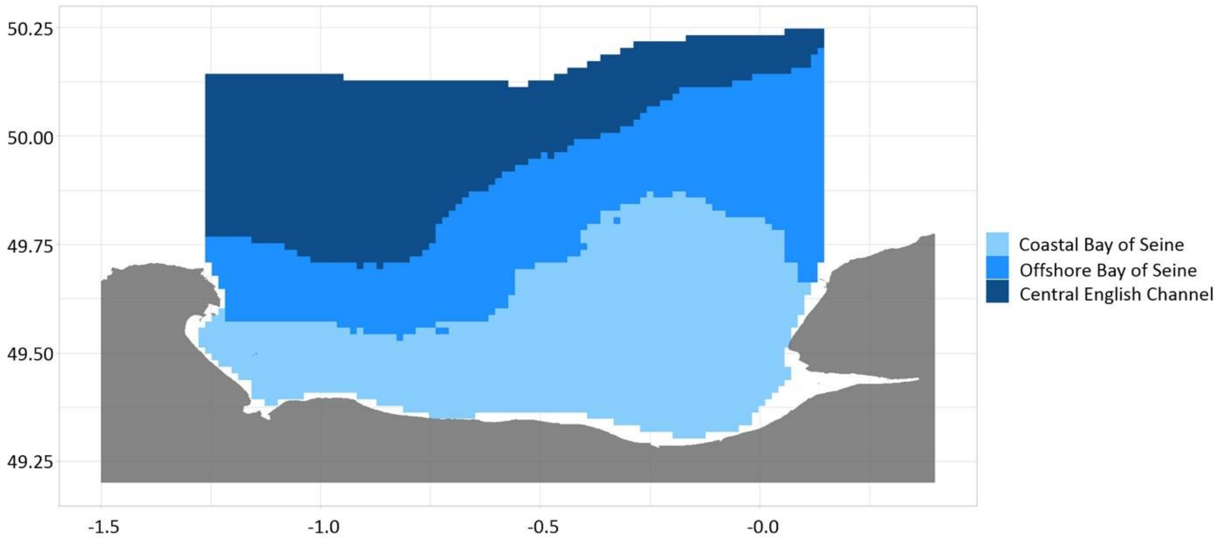

Figure - 4 Regions with similar ecosystem properties and functioning determined using a K-means clustering analysis based on the ecological network analysis index values in the reference scenario.

3.2 Effects of climate change and fishing on the functioning and organization of the system

Climate change scenarios displayed much larger variation in their ENA indices than fishing scenarios did. The CC 2100 scenario was the one with the highest number of strong variations with the reference scenario (| ∂Cliff | > 0.474, Figure - 5). While fishing scenarios had logical effects on ENA indices, with opposite responses to the increased or decreased fishing pressure, CC scenarios had surprising effects. For example, the 2050 CC scenario increased the SOI of the Coastal Bay of Seine region, while the 2100 CC scenario greatly decreased it (Figure - 5). This is linked to the different effects of climate change on the groups of the Ecospace model (Supplementary materials Table S – 37 to S - 52).

All but two indices displayed medium to strong variation in the 2100 CC scenario. Flow diversity (H) in the Central English Channel region and recycling (FCI) in the Offshore Bay of Seine region were the only indices displaying negligible variation compared to the reference scenario (Figure - 5). In the 2050 CC scenario, six indices displayed negligible variation compared to the reference scenario, especially in the Offshore Bay of Seine (3 indices) and the

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Central English Channel (2 indices) (Figure - 5). Variations due to the 2050 CC scenario were small or negligible. This difference between the 2050 and 2100 scenarios is linked to the greater effect of climate change on the trophic group's habitat suitability in the 2100 scenario than in the 2050 scenario (Supplementary materials Figure S - 41).

In general, the Coastal Bay of Seine region was the most sensitive area to CC (in both the 2050 and 2100 scenarios), with negligible variation of only one of its ecological indices, followed by the Central English Channel (3 indices) and finally the Offshore Bay of Seine (4 indices).

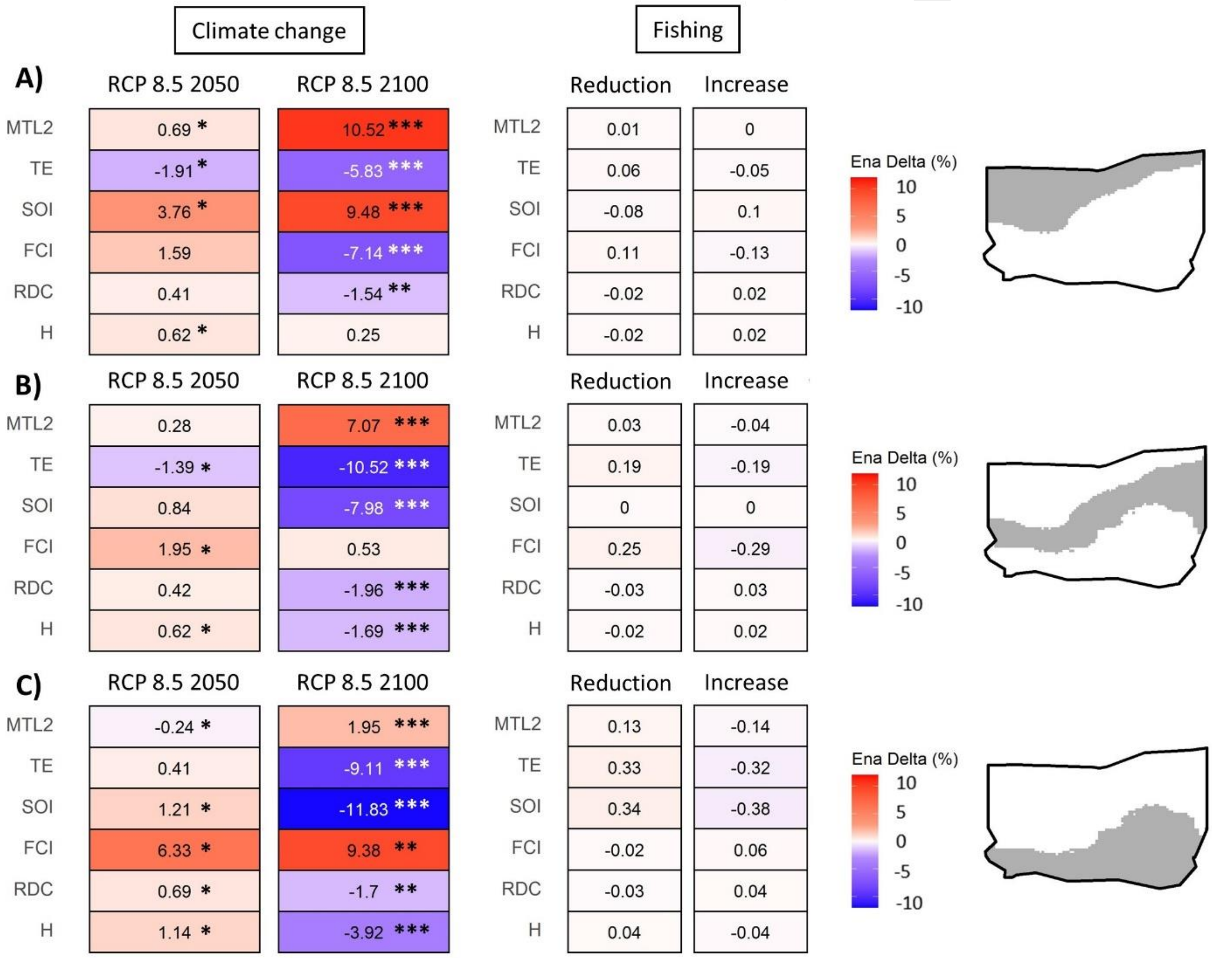

Figure - 5 Variations between the reference scenario and the different CC scenarios (left columns) and Brexit scenarios (right columns).

Positive variations are in red boxes, and negative variations in blue boxes. A), variation in the Central English Channel region; B), variation in the Offshore Bay of Seine region; C), variation in the Coastal Bay of Seine region. Cliff Delta results: *** strong variation (| ∂Cliff | > 0.474); ** medium

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variation (0.33 < | ∂Cliff | < 0.474); * small variation (0.147 < | ∂Cliff | < 0.33); no *, negligible variation (| ∂Cliff | < 0.147).

3.3 Effect of the offshore wind farm on the system

The effect of the OWF was the most visible one on the SOI of the eBoS model, followed by the mean trophic level, trophic efficiency, flow diversity, the relative redundancy of the flows, and recycling. Spatially speaking, the effects were mainly localized within the OWF perimeter, where all the above-mentioned indices increased, except recycling that was slightly reduced compared to the reference scenario (0.147 < | ∂Cliff | < 0.33) (Figure - 6). While recycling did not appear to be impacted by the OWF in the spillover regions, flow diversity, omnivory, trophic efficiency and the mean trophic level decreased. The spillover regions always resulted in a decreased metric, regardless of ENA indices, in diverse proportions. The rest of the bay of Seine did not show any significant variation between the OWF and reference scenarios, indicating that the OWF had a localized effect on the Bay of Seine ecosystem.

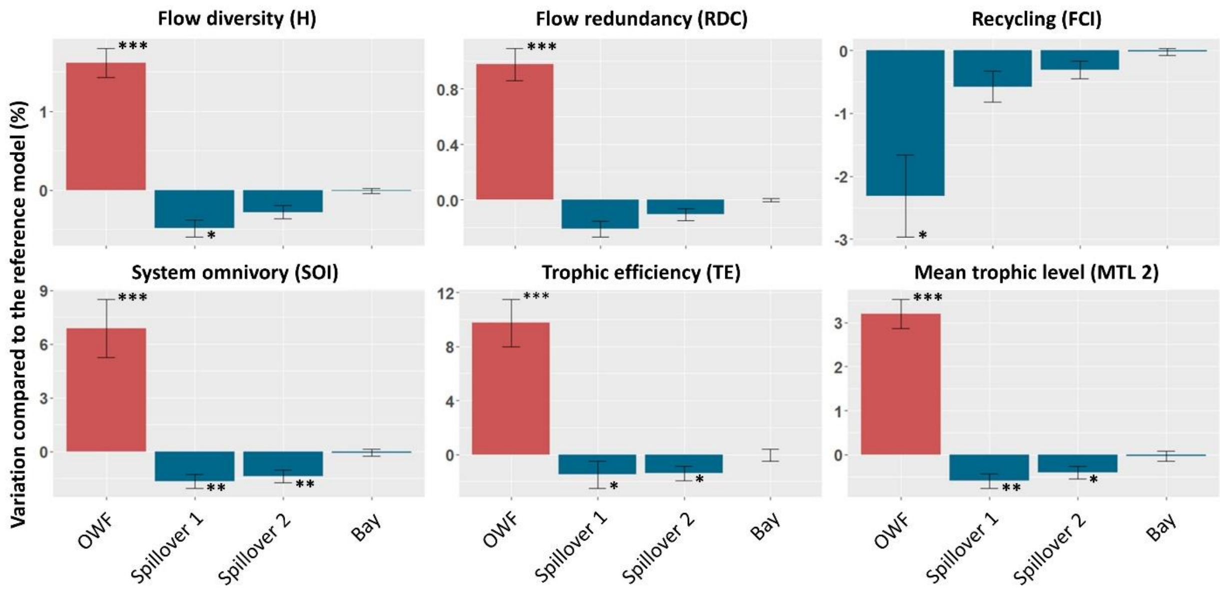

Figure - 6 Variations between the reference and OWF scenarios for the OWF sub-region.

Regions include the spillover 1 region (first two rows of cells around the OWF), the spillover 2 region (next two rows of cells around the OWF) and the rest of the bay. All sub-regions are exclusive, with no overlapping. Red bars, positive variations; blue bars, negative variations. Cliff Delta variation: *** strong (| ∂Cliff | > 0.474); ** medium (0.33 < | ∂Cliff | < 0.474); * small (0.147 < | ∂Cliff | < 0.33); no *, negligible (| ∂Cliff | < 0.147).

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4 Discussion

The modeling approach implemented in the present study improved the simulation of multiple drivers, using whole ecosystem approaches based on a single reference model. We did not represent the entire effect of CC, but rather tried to progressively improve the forecasting previously achieved in the Bay of Seine (Bourdaud *et al*., 2021; Halouani *et al*., 2020; Nogues *et al*., 2020; Raoux *et al*., 2019). Despite improvements such as modeling the reef effect of the OWF, modeling the effects of climate change on species physiology (through the habitat capacity), adding variability in the fishing regimes, there still remains limitations related to the great complexity of climate change and of its impacts on ecosystems (Hoegh-Guldberg and Bruno, 2010; Ainsworth *et al.*, 2011). Such limitations include the failure to account for the arrival of tropical non-indigenous species (NIS) in the eBoS (Cheung *et al.*, 2009; Weatherdon *et al.*, 2016). Modeling the inflow of non-indigenous species due to CC in an open system like the Bay of Seine is a very hard task. The results are often hypothetical and subject to many modeling hypotheses (Morin and Thuiller, 2009; Beaugrand *et al.*, 2018; Le Marchand *et al.*, 2020). Moreover, the arrival of non-indigenous species is often modeled with new trophic groups (Libralato *et al.*, 2015; Corrales *et al.*, 2018), which change the system aggregation. Comparing the system before and after the arrival of NIS using ecological network analysis becomes tricky, as some ENA indices are highly sensitive to the system aggregation (Johnson *et al.*, 2009). That is why we chose not to integrate such arrivals for the time being, even though NIS might have several effects on the food web structure (Libralato *et al.*, 2015; Kotta *et al.*, 2018).

Another important effect of CC on marine and coastal ecosystems is its potential impact on phytoplankton primary production (Winder and Sommer, 2012). So far, primary production models have not foreseen a clear trend of primary production in the Bay of Seine related to CC (Holt *et al.*, 2016). Moreover, turbidity is expected to be the main limiting factor of primary production in the Bay of Seine (Pascal Claquin, pers. com., UMR Borea), but the responses of current turbidity models are not consistent enough for us to predict potential primary production changes in the eBoS (Fettweis *et al.*, 2012; Capuzzo *et al.*, 2015; Wilson and Heath, 2019). Therefore, data availability did not enable us to model the effect of CC on all the groups of the model, we thus focused on the effect of CC on the distribution and

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dynamics of local macro-organisms and its effects on the ecosystem functioning (Harley *et al.*, 2006).

This study also aimed to build a framework for future studies on cumulative impacts using ENA indices. The methodology had to be simple in order to be compatible with complex cumulative assessment methods. Taking into account the uncertainty of the Ecospace model — through Monte Carlo analysis of the Ecopath pedigree — and the niche model results — through a sensitivity analysis of the niche model results — requires a large number of simulations. The long time needed to compute ENA maps and the large number of scenarios necessary for cumulative effect assessment (CEA) would make a study of uncertainty incompatible with CEA based on ENA indices. However, taking the uncertainty around the niche model results into account could represent a significant improvement for future works (Payne *et al.*, 2016), but will first require significant work to optimize the computation time of ENA indices.

4.1 Climate change and species distribution: consequences on food web functioning

The potential effects of CC on species distribution appear to have a strong structuring effect on the eBoS community in the different functional regions of the eBoS. These structural changes are clearly visible in the reduced trophic efficiency of nearly all the regions of the eBoS under both CC scenarios, except for the Coastal Bay of Seine region in the 2050 CC scenario. This implies that CC would reduce the efficiency of the ecosystem in the processing of energy through its trophic levels (Lindeman, 1942). Trophic efficiency is widely used to tackle the effects of multiple stressors, with a broad range of responses (Coll *et al.*, 2009; Niquil *et al.*, 2014b). Lower trophic efficiency can be linked to a possible ecosystem shift caused by invasive species (Baird *et al.*, 2012). Trophic efficiency in the present study seems to indicate a similar major modification of the ecosystem, regardless of the region, leading to lower efficiency and requiring a higher energy input to maintain medium to top trophic level species. This lower trophic efficiency is likely caused by the shift toward a more fish-based system (Supplementary materials Figure S - 41), as fish allocate more energy to maintenance and thus have a lower trophic efficiency than smaller invertebrates (Gillooly *et al.*, 2001). Such a structuring effect of CC due to community shifts has already been observed and is expected to play a major role in the future evolution of marine ecosystems (Walther *et al.*, 2002; Parmesan, 2006).

The structuring effect of climate change in the 2100 RCP8.5 scenario seems to result from important community changes that lead to a lower resistance of the system to disturbances. Community changes are visible through the increased mean trophic level of the system and coincide with decreased benthic invertebrate biomass as well as modified fish biomass (Supplementary materials Figure S - 41). This is the result of the high sensitivity of multiple benthic invertebrates species to CC (Rombouts *et al.*, 2012), as well as the high vulnerability of low-trophic-level fish to changing climate conditions (McLean *et al.*, 2018), making them potentially highly sensitive to CC. Taken together, the decreased biomass of low trophic level groups like invertebrates and small fish will reduce the mean trophic level and result in a loss of redundant trophic pathways, leading to a lower relative redundancy of the flow in the system. Such changes have been related to losses in the ability of the system to adequately respond to external pressure by reconfiguring itself (Odum, 1985; Ulanowicz, 1986). Losing this ability makes a system less resilient to stressors, as described by Heymans and Tomczak (2016). It is well known that invertebrates are going to be highly impacted by CC (Kendall *et al.*, 2004; Byrne, 2011). However, few studies have investigated the overall effect of community changes on ecosystem functioning. Our results support the idea that benthic communities could play a major role in the resilience of the eBoS ecosystem (Nogues *et al*., 2020; Raoux *et al*., 2019).

We predict that the effects of climate change at the 2100 horizon could result in important local variations of the system omnivory and recycling indices between the Coastal Bay of Seine and the Central English Channel regions. These variations could be attributed to the local shift of the ecological community within the eBoS. The increased system omnivory index in the Central English Channel region can be explained by the northward movement of omnivorous fish groups like benthos feeders' Gurnards (Supplementary materials Figure S - 41 & 48) rather than by the changing omnivory of the groups between the regions (Supplementary materials Table S - 11). In an opposite trend to fish, the biomass of invertebrates decreased in the Central English Channel region and increased slightly in the Coastal Bay of Seine region (Supplementary materials Figure S - 41). This is reflected on the

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system through an increased recycling in the Coastal Bay of Seine region and a reduced one in the Central English Channel region, as invertebrates play a key role in recycling. Some studies have already pointed out the overall effect of changing species distribution on ecosystem functioning (Corrales *et al*., 2018; Libralato *et al*., 2015). The present study shows that effects on the ecosystem can also be local, leading to variable ecosystem properties at a regional scale.

Modifications of the ecosystem are smaller in the 2050 CC scenario than in the 2100 scenario. They are also different for many indices in each functional region of the model. Out of the six ENA indices for the three functional regions, only five out of eighteen cases had similar responses in the two CC scenarios. The limited number of proportional responses between the 2050 and 2100 scenarios is a potential sign of the non-linear effect of CC on ecosystems. While this is partly linked to the niche model themselves and to their predictions of species suitability experiencing a range drift related to the loss of suitable climatic conditions between 2050 and 2100, as observed in other studies (Ben Rais Lasram *et al.*, 2010; Albouy *et al.*, 2013; Hattab *et al.*, 2014), this might also be caused by the cascading effects on the system (Carpenter *et al.*, 1985).

Although CC effects in the 2050 scenario are less visible than in the 2100 scenario, local trends can still be outlined. While the model forecasts a decrease of the mean trophic level in the Coastal Bay of Seine region, an increased mean trophic level is expected in the Central English Channel region. This gradient can be explained by the increase of invertebrate biomass values in the most coastal region, increasing flow redundancy and recycling (Supplementary materials Figure S - 42). In the more offshore Central English Channel region, a loss of invertebrate biomass results in a decreased invertebrate / fish ratio (Supplementary materials Figure S - 42). This modification of the ecological communities is noticeable at the ecosystem level *via* a higher mean trophic level and a lower trophic efficiency. While the 2100 scenario appears to be impacted both globally (at the entire eBoS scale) and locally (inside the eBoS), the impact of CC seems more local in the 2050 scenario with no homogeneous effects at the entire eBoS scale. This is why it is crucial to take the effects of CC into account both globally and locally. Detecting such effects at the community level might be an issue for many local development actors as they prefer to use "tailor-made" solutions, specific to their case study, that may fail to detect holistic ecosystem changes (Hendriksen *et al.*, 2014). ENA showed that by using a spatialized model, they could characterize and understand the effects of CC on the ecosystem between functional regions (local effects) and across the whole eBoS (global effects). This represents a societal priority for us to be able to predict the evolution of marine ecosystems (Claudet *et al.*, 2020). Information about the local effect of CC could prompt local stakeholders to set up actions in the field of vulnerability and adaptation of the societal system (Charles, 2012) and to raise awareness at a local scale (Ireland and Clausen, 2019).

4.2 ENA indices in fishing scenarios

While the effects of CC on the ecosystem are not proportional between the 2050 and 2100 scenarios, with strong but sometimes completely different effects on some indices, fishing has negligible but proportional effects, opposite in the two Brexit scenarios (fishing increase / decrease). The trophic efficiency and the mean trophic level have already been used in many studies to describe the effect of fishing on the ecosystems (Libralato *et al.*, 2004, 2010; Coll *et al.*, 2009). On the other hand, the mean trophic level was popularized by Pauly *et al.* (1998) and his "Fishing down the marine food web" theory that depicts the mean trophic level as sensitive to the effect of fishing, i.e. decreasing with the fishing pressure due to the decreased predator biomass. The omnivory index was also promoted as a robust index to detect the effect of fishing (Fulton *et al.*, 2005). Despite the many items of evidence of their operational ability to describe the effects of fishing, ENA variations due to fishing were consistently considered negligible by the Cliff Delta. The little sensitivity of ENA indices to fishing scenarios might thus result from the little impact of the Brexit scenario on ecosystem functioning. The eBoS is a heavily anthropized ecosystem, with a strong fishing industry (Buléon and Shurmer-Smith, 2021). Protecting the ecosystem from the effects of fishing might require ambitious management plans to truly help ecosystems recover (Dunford *et al.*, 2004).

4.3 Effect of the offshore wind farm on the extended bay of Seine

As observed by Halouani *et al*. (2020) who simulated the possible reserve effect in the case of fishery closing in the entire OWF area, it appears that the OWF could play the role of a "fish aggregating device". The aggregating role of the OWF appears to have an important structuring effect on the ecosystem. The structuring role of the OWF is particularly prominent with the increased mean trophic level, trophic efficiency, omnivory and redundancy of the

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flows. The aggregating effect is also noticeable outside the OWF perimeter. Biomass outside the OWF appears lower in the OWF eBoS scenario than in the reference scenario. This decreased fish biomass is likely due to the agglomeration of the mobile fish groups inside the OWF area due to the higher suitability of the cells and to the higher prey density for fish groups inside the OWF. Agglomeration is well known and has been extensively studied (Bohnsack, 1989; Pickering and Whitmarsh, 1997; Smith *et al.*, 2015) and was also observed by Halouani *et al*. (2020) to be caused by the reserve effect only (Colléter *et al.*, 2014).

Inside the OWF perimeter, Ecospace predicted a similar structuring effect to the one forecasted in Nogues *et al*. (2020). This structuring effect is visible through the many important modifications of the ecosystem, which appears to shift toward a more demersal / benthic system (Supplementary materials Figure S - 45). Similarly to the results of Raoux *et al*. (2019), the OWF could increase the relative redundancy of the flow. The OWF of the eBoS model may also increase the omnivory index of the system, as observed by Nogues *et al*. (2020). However, unlike previous studies, recycling is reduced by the OWF in our simulations. All these modifications – along with the increased trophic efficiency and the increased flow diversity – seem to be linked to an increased resistance of the system to disturbance. With the higher flow redundancy, the system has more in store against disturbances (Levin and Lubchenco, 2008), improving its ability to adapt and overcome stresses. The higher omnivory index also suggests that the system would be more resilient, as it makes it more flexible (Fagan, 1997; Libralato, 2013). The heterogeneity brought by the hard substrate of the wind turbine structure to the sandy habitat surrounding the OWF seems to increase the flow diversity. Flow diversity can be interpreted as species diversity (Christensen, 1995). Therefore, an increase in habitat heterogeneity should also increase local diversity (Munguia *et al.*, 2011). These changes are all linked to the increase in benthic and demersal biomass (Supplementary materials Figure S - 45), which tends to have an overall positive impact on the ecosystem of Courseulles-sur-Mer by making it more complex, efficient, diverse and resilient (Nogues *et al*. 2020).

Changes in the eBoS system are also visible outside the OWF area. Through the agglomeration of fish species in the OWF area, fish biomass may decrease in the vicinity of the OWF. Even though these biomass changes are small, they still have an effect on ENA indices

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and on the ecosystem. Decreased fish biomass and increased invertebrate biomass lead to a lower mean trophic level as well as a lower omnivory index of the system around the OWF (Supplementary materials Figure S – 45).As trophic efficiency and flow diversity also appear to decrease, these results tend to indicate a simplification of the ecosystem around the OWF toward a less resilient state. However, because fishing could increase inside the OWF due to the reef effect (see above, Grossman *et al*., 1997), fishing may also increase in the surrounding areas of the OWF, potentially affecting an already weakened system. This emphasizes the need for careful planning of fishing around and inside the OWF area and may require mitigation, even in such a limited space. With these new insights into the spatial footprint of multiple drivers on the ecosystem, ENA indices demonstrate their usefulness to locate areas in need of careful ecological management (Safi *et al.*, 2019). ENA indices could be used to i) plan spatial management projects based on the responses of the ecosystem to drivers and ii) better maintain ecosystem sustainability (Curtin and Prellezo, 2010).

Conclusion

For the first time in ecological network analysis, the mapping of ENA indices provides insights into spatial ecosystem functioning. ENA indices further prove their usefulness and potential as tools for ecosystem management by helping us understand human induced ecosystem changes. Therefore, they could be used to support marine spatial planning by highlighting areas of concern where the ecosystem could be more sensitive to perturbations. Their ability to detect the effects of localized and more global ecosystem drivers on ecosystem functioning could be used to link local and global ecosystem management initiatives. It is also important to note that these scenarios were built to test the ability of ENA indices to assess cumulative effects (Nogues *et al.*, in prep.). There is an increasing demand for studying the combined effects of climate change and other drivers at the whole ecosystem scale in order to predict ecosystem changes and elaborate management scenarios. This study sets the basis for such work: it provides tools for simulating the effects of multiple drivers, which then need to be combined, to determine the potential cumulative effects resulting from interactions between the different anthropogenic drivers.

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Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Author contribution

All authors developed the ideas, conceptualized and revised the manuscript. Q.N. was the lead author and main contributor. E.A., G.H., P.B. and Q.N. build the model. E.F., F.L.T., N.N. and Q.N. built the scenarios.

Competing interest statement

The authors have no conflict of interest to declare.

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