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The usefulness of food web models in the ecosystem services framework: Quantifying, mapping, and linking services supply

Nogues Quentin [1, *], Baulaz Yoann [2], Clavel Joanne [3], Araignous Emma [2], Bourdaud Pierre [4],
Ben Rais Lasram Frida [5], Dauvin Jean-Claude [6], Girardin Valérie [7], Halouani Ghassen [8],
Le Loch Francois [4], Loew-Turbout Frédérique [9], Raoux Aurore [6], Niquil Nathalie [1]

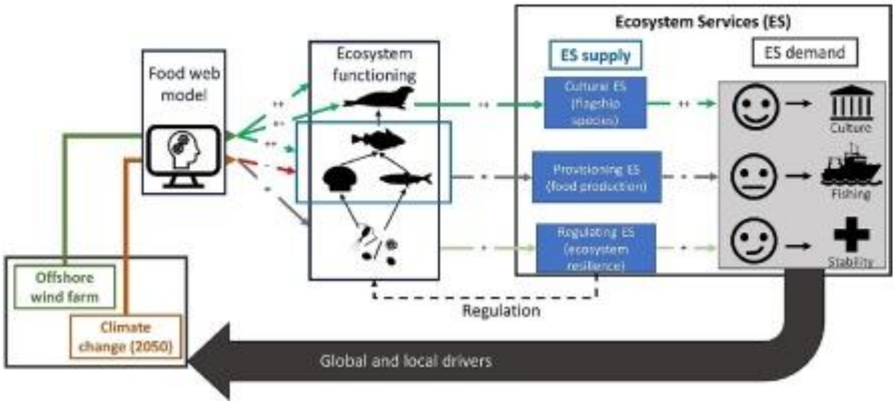
[1] Normandie Univ, UNICAEN, UMR 8067 BOREA (CNRS, MNHN, UPMC, UCBN, IRD-207), Caen CS 14032, France
[2] France Energies Marines ITE-EMR, 525 Avenue Alexis de Rochon, Plouzané 29280, France
[3] Laboratoire Dynamiques Sociales et Recomposition des Espaces, LADYSS, UMR 7533, Univ. Paris, Paris 75205 Cedex 13, France
[4] Univ. Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, rue Dumont d'Urville, BP 70, Plouzané 29280, France
[5] Univ. Littoral Côte d'Opale, Univ. Lille, CNRS, IRD, UMR 8187 LOG, Laboratoire d'Océanologie et de Géosciences, Wimereux F 62930, France
[6] Normandie Univ, UNICAEN, CNRS, UMR 6143 M2C, 24 rue des Tilleuls, Caen CS 14032, France
[7] Normandie Univ, UNICAEN, CNRS, UMR 6139 LMNO, 6 Bd Maréchal Juin, Caen CS 14032, France
[8] Ifremer, Unité halieutique Manche-Mer du Nord Ifremer, HMMN, Boulogne sur mer 62200, France
[9] Normandie Univ, UNICAEN, MRSH, Caen CS 14032, France

* Corresponding author : Quentin Nogues, email address : quentin.nogues33@gmail.com

Abstract :

Coastal ecosystems provide a wide range of valuable ecosystem services (ES) for human wellbeing. Such services depend on the functioning and structure of ecosystems. Unfortunately, these ecosystems are threatened by humans, directly impairing their ability to provide these services. In order to predict such changes, we used a food web model to forecast potential spatial changes in ES supply in the Seine Bay (English Channel), due to climate change effects (CC) and the setup of an offshore wind farm (OWF). Three ES were studied, food production from fishing, top predator production for cultural purposes and the potential resistance of the ecosystem inferred from its organization. The ability of the Seine Bay ecosystem to produce food appears to be negatively impacted by the effect of climate change. Because of the important economic role of fishing in Normandy, such changes could percolate on the entire social and economic system of the bay. The Courseulles-sur-Mer offshore wind farm appears to increase the supply of services and limit the impact of climate change at the local spatial scale, which could give stakeholders insights into mitigating the effects of climate change. Such ecosystem approach enables for a more integrative view of ES supply, through the characterization of the entire system functioning.

Graphical abstract



Highlights

► Food web models are ideal tools for Ecosystem services (ES) assessment. ► The coastal part of the Seine Bay appears to play a key role for ES supply. ► In the Seine Bay, climate change seems to have a negative effect on fished species, thus reducing food production. ► Locally, the offshore wind farm reef and reserve effects appear to dampen the negative effect of climate change, and even seem to increase ES supply. ► Anthropogenic drivers' interactions should be considered when estimating changes in ecosystem services supply.

Keywords : Ecosystem services supply, Ecosystem functioning, Ecological network analysis, Ecosystem change, Cumulative effects, Mapping

1 Introduction

Marine and coastal ecosystems are of great importance for societies around the world as they provide many ecosystem services (ES) of high values (Galparsoro et al., 2012; Martínez et al., 2007). Unfortunately, these ecosystems are highly threatened by anthropic activities. Indeed, more than half of all humans live at least 200 kilometers from the coast (Kennish, 2002; UNEP et al., 2012), which puts a tremendous pressure on them, through fishing or habitat destruction, among others. Such pressures may threaten the supply of ES and thus change our relationship with nature (MEA et al., 2005; Worm et al., 2006). In order to better manage such changes, we need to adequately quantify the supply of ES (De Groot et al., 2010), as well as their evolution in the face of changes resulting from multiple anthropic drivers like climate change (CC), fishing, and marine renewable energies, among others. We need to develop holistic approaches that can properly model the effects of a wide range of drivers on whole ecosystems, on their structure and organization, and more importantly for ES, their functioning (De Groot, R.S., 1992; Duncan et al., 2015; Hein et al., 2006).

Modeling marine ecosystems as interconnected systems is necessary to accurately portray their dynamic and functioning (Shurin et al., 2006), with changes in one part of the system often cascading throughout the whole system. Ecosystem-based management has been described as the solution needed to enable a sustainable exploitation of marine ecosystems (Buhl-Mortensen et al., 2017; Gregory et al., 2013), and in an ecosystem services (ES) framework, to better maintain the supply of a wide range of ES (Beaumont et al., 2007). Indeed, the supply of ES depends on the functioning of the entire ecosystem, and many ecological groups may play a significant role supplying ES, at a wide range of scales (Kremen, 2005). Using ecosystem approaches to quantify ES thus responds to the demands of stakeholders in the management and monitoring of the marine environment, to adequately predict potential changes in the functioning of coastal ecosystems.

Food web models are ideal Ecosystem-based management tools as they quantify trophic interactions in marine ecosystems (predator prey relationships). They can quantify many aspects of ecosystems, from structural information (biomasses) to, here, more informative functional information like energy flows between ecological groups, providing knowledge about the ecosystem functioning (Thompson et al., 2012). They can thus quantify the secondary production of any ecological group in an ecosystem and the effective activity of such group in providing a said ES (Beaumont et al., 2007; Duncan et al., 2015). Moreover, information other than group production can also be quantified using ecological network analysis (ENA). With network analysis, more complex information relying on the trophic pathways of the entire food web can be computed. This is used to better understand the properties of an ecosystem (Finn, 1976; Libralato, 2013; Ulanowlcz and Norden, 1990; Nogues et al., 2022). They can be linked to emerging properties of ecosystems like maturity or ecological resilience which are inherently linked to the ecosystem functioning (Bondavalli et al., 2006; Christensen, 1995; Saint-Béat et al., 2015). Food web models can thus help assess a wide variety of ES, while keeping an integrative view of ecosystems and considering their inherent complexity.

Food web models have been widely used to study human impacts on ecosystems. These models were applied to the Bay of Seine to simulate the ecosystem effects of different anthropogenic pressures and enhance our understanding of ecosystem functioning (Halouani et al., 2020; Raoux et al., 2017; Tecchio et al., 2016). However, despite the improved capabilities of food web models in the last years, the effects of anthropogenic pressures were often limited to fishing pressure (Kytinou et al., 2020). The wide range and diversity of outputs they provide could help to better address the diversity of human-nature relationships such as the cultural ES category (looking at specific species or hole ecosystem parameters like diversity), which has often been neglected (Blicharska et al., 2017). Integrating social sciences into ecological research has become a top issue in the ES scientific community (Collins et al., 2011; Redman et al., 2004). Extensive theoretical work has been done on food webs, providing a great deal of knowledge about ecosystems and their regulatory mechanisms (Frederiksen et al., 2006; Menge, 2000). However, the link between complex quantitative approaches and values related to human-nature relationships are rarely mobilized in the ecosystem services literature, and even less so in ES assessment works.

In this paper, we show the usefulness of Ecospace, a spatial food web modeling approach, to quantify the supply of several ES in the extended Seine Bay (eBoS) in the English Channel. This work is not intended to extensively quantify each ES supplied by the eBoS ecosystem, but rather to show the potential of food web models to quantify ES supply using functional model outputs. One service from each category of ES of the CICES (*Common*

International Classification of Ecosystem Services) was chosen (Haines-Young and Potschin, 2018), each depending on different biotic component (either species or group of species). After selecting the most suitable indices — from basic production output to a more complex network index — we quantify the actual supply of each of these ES and map the eBoS based on its ability to provide the selected ES. We identify spatially which of the functional regions of the eBoS play a key role in ES supply. We use insights from previous works on the eBoS to model the potential effects of CC and of an offshore wind farm (OWF) on the supply of the selected ES. Furthermore, we combine CC and the OWF to determine their cumulative effects on the selected services. Finally, we discuss the utility of food web models in quantifying ES, their benefits and especially their ability to bring an environmental view to the ES framework.

2 Materials and methods

2.1 Study area

The extended Seine Bay (eBoS) is a sea space enclosed between the Cotentin peninsula on the west and the 'Pays de Caux' in Normandy, on the east. South of the eBoS is the Calvados Coastline in France and north is the French-British delimitation of the Exclusive Economic Zones (Figure - 1). It is a shallow coastal system open on the north to the English Channel, with a mean depth of 35 m. Notable geomorphologic features include the Seine estuary south-east of the eBoS and the Seine estuary paleo-valley on the north-west (Dauvin, 2015). The eBoS ecosystem can be divided into three functional regions, from coast to offshore, with the most coastal regions being the most productive and most ecologically diverse (Nogues et al., 2022). This is reflected in the ecosystem functioning of these regions, with the most coastal region being more resilient and complex than the offshore ones. Other structural sub-regions were also defined, inside the OWF (OWF), and around it (spillover zone). These regions were defined to help distinguish the effects of the different drivers on the ecosystem.

The eBoS ecosystem, inside the English Channel, with a ship entering or leaving it every ~ 10 minutes, is one of the busiest shipping corridors in the world with 20% of the global maritime transport (Buléon and Shurmer-Smith, 2021). Its coastlines are densely populated with densities often reaching 500 inhabitants/km², a significant population living in close proximity of the eBoS and benefiting from its ES, the eBoS is home to a wide variety of anthropic activities (Buléon and Shurmer-Smith, 2021; Dauvin et al., 2020). The Normandy coastline is an important known tourism area: mainly recreational (marinas, seaside resorts, "blue flag" label, sailing, *etc.*), historical and cultural (World War II landing beaches being classified as a UNESCO World Heritage Site, Viking invasions, museums and maritime heritage, *etc.*), and also natural (animal watching, hiking, coastal paths, *etc.*). Fishing plays an essential role in the eBoS, including on-foot fishing. Several big fishing ports are located in direct proximity of the eBoS; Port-en-Bessin is the port in France for king scallops fishing (more than 15,000 tons of annual catch in Normandy) and the fourth most earning fish market in France in 2016 (Buléon and Shurmer-Smith, 2021). Aquaculture activities (mussels and oysters) are also important. The eBoS sea space has important marine renewable energy perspectives (one of the largest in Europe) with two OWF under construction, Courseulles-sur-Mer (~ 50 km², 64 turbines) and Fécamp (~60 km², 71 turbines) on its east. A third wind farm will be located in Dieppe-Le-Tréport, while a fourth and a fifth OWF are also under discussion and should be located in the northwestern part of the Seine Bay. Thus, the eBoS plays a key role for many people and activities, making crucial the understanding of its ability to provide ES, and how this may evolve in response to human activities.

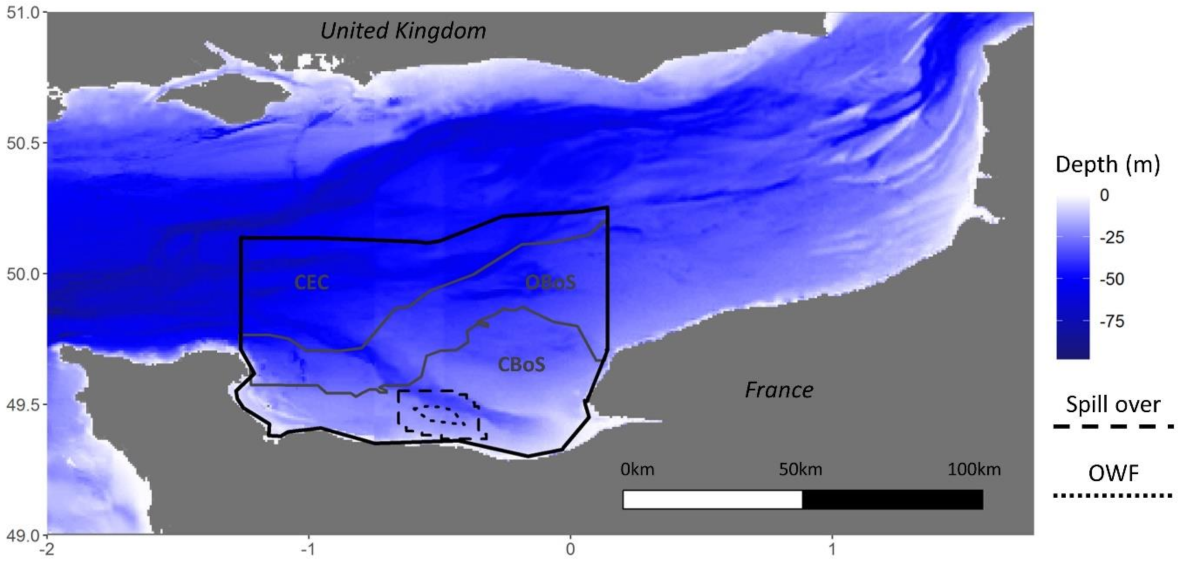


Figure - 1 Map of the extended Seine Bay (eBoS) within the English Channel.

The eBoS model is mapped with a continuous black line and includes the coastal system of the Bay of Seine from 5 meters depth to the France/UK Exclusive Economic Zone delimitation. The offshore wind farm (OWF) sub-region is mapped with a dotted line, and the spillover sub-region around the park in a dashed line. Inside of the eBoS, the functional regions of the ecosystem determined in Nogues et al., 2022 are indicated: the Central

English Channel (CEC), the Offshore Bay of Seine (OBoS) and the Coastal Bay of Seine (CBoS).

2.2 Spatial food web modeling of the eBoS using Ecospace.

Food web models are network models that represent prey/predator interactions to quantify the pathways of energy between the different ecological groups of an ecosystem (Dunne, 2006). They are composed of nodes and edges: nodes represent ecological groups, i.e., one or several species with similar ecology and trophic sources (Gauzens et al., 2015), edges are flows of energy between nodes and represent prey/predator interactions. Food web models have been created for determining ecosystem's unknowns that are hard to quantify *in situ*. Many approaches to model food webs exist in the literature (Kytinou et al., 2020), which may be static (steady-state model) or dynamic, in time and even space. In this study we used a spatio-temporal dynamic model, Ecospace, which is part of a modeling approach called *Ecopath with Ecosim* (*EwE;* Pauly et al., 2000). The *EwE* framework is composed of three models: Ecopath (steady state approach), Ecosim (time dynamic approach) and Ecospace (spatial-temporal approach).

Food web models of the eBoS were built to perform various studies of the effects of multiple anthropic activities (Supplementary materials Table S – 1, S – 2 & S - 3). A full description of the *EwE* framework used to build food web models of the Bay is available in Pauly et al. (2000). The EwE framwork is based on Ecopath. Ecopath is used to define the system topology, which includes the number of trophic groups using biomass, production, consumption and ecotrophic efficiency data, and the links between groups using species diet. Ecopath follows two main equations which set its steady state nature:

$$\text{Production} = \text{Predation mortality} + \text{fishing mortality} + \text{biomass accumulation} + \text{net migration} + \text{other mortality.} \quad (1)$$

$$\text{Consumption} = \text{Production} + \text{respiration} + \text{excretion} \quad (2)$$

The eBoS Ecopath, Ecosim and Ecospace models are composed of 42 groups, including 40 living groups and 2 non-living groups. Living groups include a large spectrum of marine species from planktivorous species to marine mammals and sea birds (Supplementary materials Table S – 4 & S - 5).

Ecosim is the time dynamic module of Ecopath (Christensen and Walters,2004). It was implemented based on parameters inherited from the Ecopath model of Bay of Seine (Halouani et al. 2020). The Ecosim model was fitted to times series of catches and biomass to calibrate the relationship dynamics between the different trophic group for the period 2000 – 2015 (Supplementary materials Table S – 2 and Halouani *et al*. 2020).

Ecospace is the spatio-temporal module of Ecopath that allows the representation of the dynamics of the different components of the ecosystem on a two-dimensional spatial grid with homogeneous cells of equal size (each cell being a dynamic trophic model). Trophic groups and fishing fleets are assigned to the different cells of the Ecospace model using environmental drivers. Trophic groups can move between the cells of the grid according to "Eularian" approach and the distribution of the fishing mortality is based on a gravity model (Walters et al., 1999, Walters et al., 2010). Ecospace can also be used for spatial management, to simulate spatial fishing regulations.

The Ecospace spatial model of the eBoS was composed of 4907 cells, each cell modeling a time dynamic Ecosim food web model and having a resolution of 0.015° x 0.015°. The distribution of the 40 trophic groups in each cell of the Ecospace was set using multiple environmental driver maps (Environmental maps and suitability maps, see (Supplementary materials Table S – 2). Environmental maps include depth map from GEBCO (Supplementary materials Table S – 2, Figure S - 1) as well as a primary production map from SeaWifs representing the relative chlorophyll a concentration in the bay in 2000 (Figure S - 2). As for suitability maps, they were added in Nogues et al. (2022) and were built from species distribution model (SDM) suitability index maps (Christensen et al., 2014; Coll et al., 2019; Supplementary Materials Table S- 2, 3 and 4). SDM are correlative approaches, which correlate species occurrences with environmental parameters to determine species habitat suitability. Species distribution models used climatic as well as habitat parameters (Ben Rais Lasram et al., 2020; (Supplementary materials Table S – 3). When ecological groups were composed of only one species, SDM outputs were directly applied to drive the group distribution while groups composed of multiple species were driven according to the weighted suitability index maps of each species, based on their biomass (Bourdaud et al., 2021). More details on the models are available in Halouani et al. (2020) and Nogues et al. (2022).

The finalized eBos Ecospace model developed in Nogues et al. (2022) is used as reference scenario and represents the current state of the ecosystem before introducing impacts induced by different anthropogenic drivers.

2.3 Anthropogenic drivers modeling

Modeling the effects of CC and of the Courseulles-sur-Mer OWF on the food web of the eBoS was made by Nogues et al. (2022) using different data sources introduced in Ecospace using built-in tools. We describe briefly the methods used here.

SDM suitability index maps were used to define species distribution and to simulate the effect of CC on species distribution. As described before, the initial distribution of species was driven by suitability index maps computed using current climatic parameters (2012 to 2015). To model the climate change effect, SDM were also run with climatic parameters from forcing scenarios of the IPCC (Intergovernmental Panel on Climate Change) (Ben Rais Lasram et al., 2020). We tested different scenarios and favored the RCP 8.5 scenario at the 2050 horizon because we considered it more realistic (Schwalm et al., 2020). For introducing suitability index maps in the Ecospace model, we used the Spatial-Temporal framework of *EwE* 6 (Steenbeek et al., 2013). This allowed us to replace the reference suitability index maps with the CC suitability index maps as environmental drivers, thus changing the habitat suitability for each species according to the expected effect of CC on the species distribution. By changing the habitat suitability and following the foraging arenas theory (Ahrens et al., 2012; Walters et al., 1997), this altered multiple predation parameters for the species and *in fine* the species vulnerability to predation, its consumption and thus its production (Christensen *et al*., 2014).

To model the potential effects of the Courseulles-sur-Mer OWF, data from previous studies on its potential impacts were introduced in Ecospace through built-in tools. Here we have decided to model the long lasting and structuring effects of the OWF on the ecosystem, thus we focused on the impact of the operational phase of the OWF (Bergström et al., 2013; Elmer et al., 2006; Koeller et al., 2006). Many sources state that the most relevant long-lasting effects of the OWF on its environment are the reef effect caused by the arrival of new hard substrate and the partial reserve effect caused by the closing of fishing activities within the OWF area (Degraer et al., 2020; De Mesel et al., 2015; Langhamer, 2012). The reserve effect of the Courseulles-sur-Mer OWF was first modeled by Halouani *et al*. (2020), of which we follow the method. In Ecospace, marine protected areas can be created by blocking fisheries access to certain cells of the grid. In this manner, 6 out of the 37 cells of the OWF area were prohibited to fishing activities as to correctly represent the OWF owners' proposal to "optimize" fishing by closing only fifteen percent of the OWF total surface (Raoux et al., 2018).

To model the potential reef effect caused by the OWF, we used results from Raoux et al. (2017), who modeled the Courseulles-sur-Mer OWF reef effect with Ecopath. There, several groups biomasses were forced as they appeared to be benefiting from the reef effect of the OWF in other parks in Europe (Supplementary materials Table S - 8). The same effects on the same ecological groups were model in the eBoS Ecospace model using new environnemental driver maps, which mirror the forcing used by Raoux et al. (2017). Thus, the habitat of the OWF was made more suitable for the species considered attracted by the OWF reef effect in Raoux et al. (2017) (the increase in biomass was translated in an increase in habitat suitability, benefiting species consumption, production and thus biomass).

Scenarios tested here thus include: the reference scenario, the offshore wind farm operation with the reef and the partial reserve effect, climate change in 2050, and all anthropogenic drivers combined.

2.4 Ecosystem services quantification

Using the previously published eBoS model, we quantified ES supply following Haines-Young and Potschin (2010 & 2018) framework and considered ES supply to be the result of ecosystem functions which determine the ''capacity of ecosystems to provide goods and services that satisfy human needs, directly and indirectly'' (De Groot, 1992). We also considered the requirements of Boerema et al. (2017) to coherently define what is quantified: is it the actual supply of ES or the potential supply of ES? The potential supply of ES refers to the capacity of the system to produce such services while the actual supply of ES defines the part used for the well-being of human population (Bastian et al., 2012).

Ecospace will produce a wide range of outputs: from structural outputs like groups biomass and trophic levels, to fishing outputs like fishing mortality, and even functional outputs like catches and trophic flows between groups when using the enaR Ecospace plugin (Nogues et al. 2022). Here we used functional outputs, either directly looking at groups production or through Ecological Network analysis (Supplementary materials Table S - 9).

Since we do not aim at an exhaustive quantification of ES supply, we decided to quantify a limited number of services, using a wide range of outputs. This was made to give insights on how food web models could be used to quantify ES supply.

The ES selected by the authors represent ES of great importance in the eBoS but also in many other ecosystems and include:

- Provisioning ES -> Food provisioning from fishing (CICES 1.1.6.1). To quantify it, we used capture flows computed from Ecospace for the fish and the invertebrate groups that we combined to quantify the actual supply of the ES (in t/km²/year). Using captures as an indicator of ES supply has been suggested in previous studies (Böhnke-Henrichs et al., 2013; Olander et al., 2018; Weijerman et al., 2018). This indicator quantifies the actual supply of ES and consider fishing capacity: availability of the targeted groups, catchability, price and distance to port for each gear type and depending on fleet activity (Walters et al., 1999). Most captured species in the eBoS include European pilchards (*Sardina pilchardus*), King scallops (*Pecten maximus*), European plaices (*Pleuronectes platessa*), small-spotted catsharks (*Scyliorhinus canicula*), mackerels (*Scomber scombrus*). For an exhaustive list of the captured species, please refer to the supplementary materials (Table S - 4).

- Regulating ES -> Ecological resilience based on food web functioning referred as “Biological control/insurance” (Baumgärtner and Strunz, 2011; Böhnke-Henrichs et al., 2013; Peled et al., 2020). In food webs, some network properties can be stabilizing. These stabilizing effects can be linked to the ‘ecological resilience’ which determines the ability of an ecosystem to maintain its original state in the context of external changes (Holling, 1996; Saint-Béat et al., 2015), and to maintain ES supply (Biggs et al., 2012; Daily et al., 1997). For the ecological resilience ES, the relative redundancy ENA index was used (RDC, no unit). ENA indices provide information on the functioning and organization of trophic networks and are computed with various equations which consider the entire flow matrix between trophic groups (Supplementary materials Table S - 9). The relative redundancy characterizes the redundancy of trophic pathways (functional redundancy). The relative redundancy (RDC or R/DC: overhead of the internal flows: R, on the development capacity: DC) can only vary between 0 and 1. A relative redundancy close to 0 indicates a very constrained and organized system (i.e., a low uncertainty around the origin of the trophic input, more akin to a food chain), while close to 1 indicates an inorganized and redundant system (i.e., a high uncertainty around the origin of the trophic input indicates redundant trophic pathways and thus a high flow diversity). Following ecological theory studies (Odum, 1953; Ulanowicz, 2018) and field experiments (e.g. Baird et al., 2007; Cardinale et al., 2002), the organization of an ecosystem seems to be a good measure of the ecosystem resilience, and thus of the actual ES supply (Biggs et al., 2012).

- Cultural ES -> Flagship species (CICES 3.2.2.1): this ES represents the existential cultural role of certain animal species. Species that people think should be conserved and have an important sentimental, imaginary, or relational intrinsic value to them. For the flagship species ES, we used the summed production of multiple top predator compartments (in t/km²/year). Species considered include Bottlenose dolphins (*Tursiops truncatus*), harbour porpoises (*Phocoena phocoena*), grey seals (*Halichoerus grypus*), harbor seals (*Phoca vitulina*) and various marine sea birds like gulls (*Larus sp*), northern gannet (*Morus bassanus*), common guillemot (*Uria aalge*) and scoters (*Melanitta nigra / Melanitta fusca*). For an exhaustive list of flagship species, please refer to the supplementary materials (Table S - 4). These species were aggregated in 6 trophic groups: three marine mammal groups (dolphins, seals, and harbour porpoises) and three sea bird groups (Surface feeding birds, benthic feeding birds and plunge and pursuit birds). The ES indicator was the sum of both birds and marine mammals' production (components of the cultural index). We selected such species based on preliminary results from current research studying humans and biodiversity relationships through ethnographic inquiry and quantitative survey (Sensitroph, n.d.). Due to the difficulty in quantifying the interactions between the production of flagship species and humans, for the benefit of cultural enhancement (Blicharska et al., 2017), this indicator is thus more akin to the potential supply of ES.

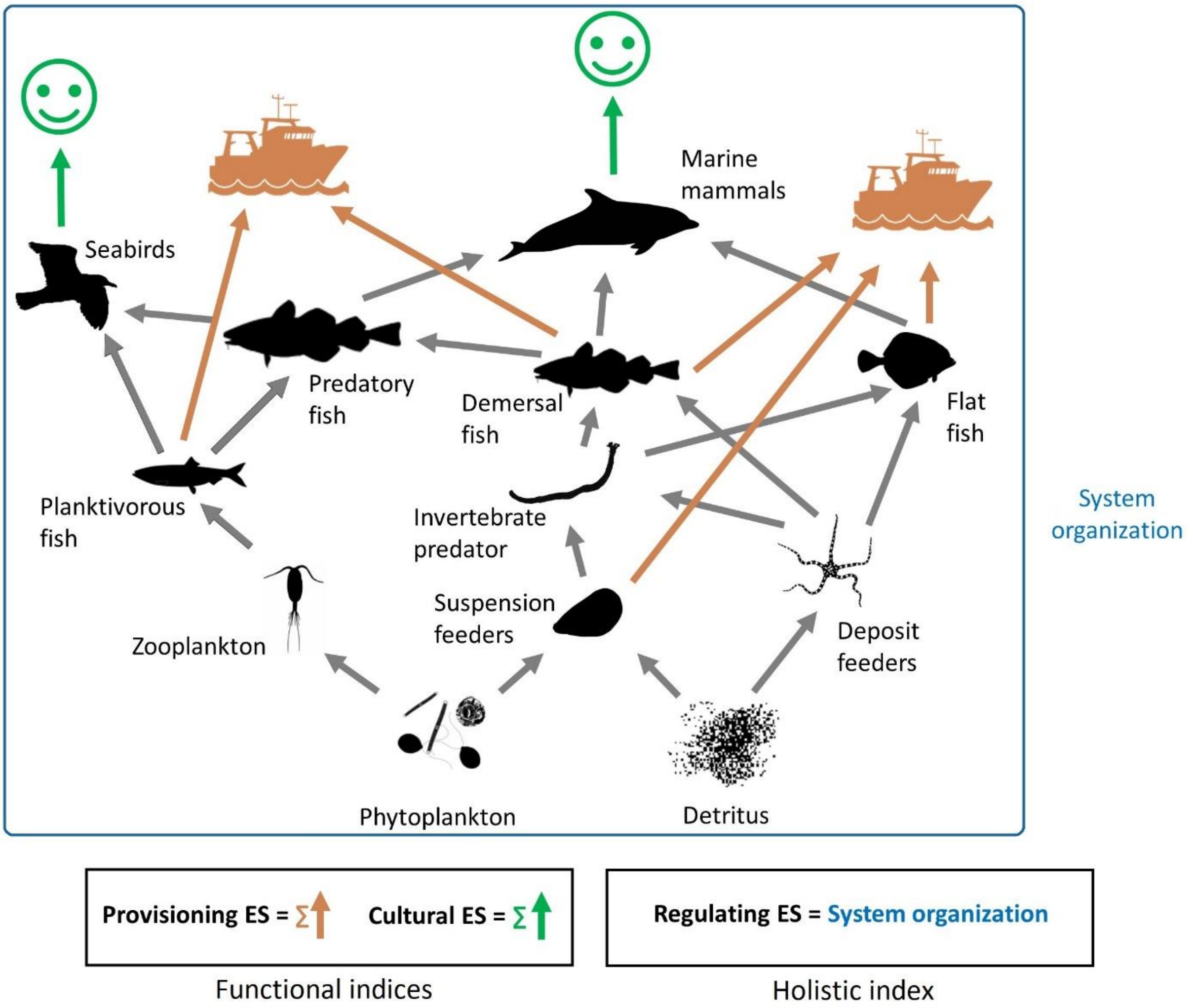


Figure - 2 Diagram of ecosystem service supply indices in the food web.

Schematic of the food web, representing trophic groups (icons) and energy flows (arrows). Indicators can be divided in two main groups: functional index (energy flows or arrows: catches in orange and flagship species production in green), and holistic index (entire ecosystem properties: regulating ES). A detailed description of the equations used is provided in supplementary materials (Table S - 9).

2.5 Evolution and mapping of ES supply in the eBoS.

Indicators of ecosystem services supply were computed for the reference scenario, the CC scenario, the OWF scenario and the combined CC and OWF scenario. Each scenario was then compared to the reference one to determine the separate and combined impacts of anthropogenic drivers. This aims to get an overview of the area producing ES, and to determine the effects of either CC and/or of the OWF on the ES supply, as well as their potential cumulative effects. Components were also compared to explain potential changes in ES supply.

Indicators quantifying the supply of each ES were mapped for each scenario tested in the eBoS. To better analyze the evolution of ES supply, we partitioned the eBoS based on previously determined functional regions and structural sub-regions (Figure - 1).

To determine whether the effect of each driver (CC or OWF) on the ES supply was important, a Cliff Delta was calculated to compare the indicators of the reference Ecospace scenario with the scenarios modelling one of the two drivers, for each region of the model. The Cliff delta is a non-parametric effect size metric that quantifies the amount of difference between two groups of observations (Cliff, 1993; Tecchio et al., 2016). It was previously used to compare ENA values inside the eBoS (Nogues et al., 2020) and the same threshold values threshold as Romano et al. (2006) were kept (negligible if the Cliff Delta (| ∂Cliff |) was < 0.147, low if 0.147 < 411 | ∂Cliff | < 0.33, medium if 0.33 < | ∂Cliff | < 0.474, or strong if | ∂Cliff | > 0.474).

To characterize the cumulative effects resulting from CC and the OWF on the ES supply, the individual effects (ΔI_s^{sep}, eq.3) of each driver were summed to determine the additive effect of both CC and the OWF ($\sum \Delta I_s^{sep}$).

$$\Delta I_s^{sep} = \frac{I_s - I_r}{I_r} \tag{3}$$

where I_r is the index value of the reference model and I_s the index value of a single-effect model (OWF only or CC only).

The additive effect ($\sum \Delta I_s^{sep}$) was then compared to the combined effect (ΔI_C^{cum}, eq.4) of both drivers to determine cumulative effects resulting from the interaction of CC and of the OWF on the ES supply (Figure - 33, Fu et al., 2018; Nogues et al., 2020; Travers-Trolet et al., 2014). This comparison was made for each functional and structural region of the eBoS. To determine if the cumulative effect was relevant on the said supply of ES, the Cliff delta was used to compare the additive effect to the combined one, for each region and ES supply indicator.

$$\Delta I_c^{cum} = \frac{I_c - I_r}{I_r} \tag{4}$$

where I_r is the index value of the reference model and I_s the index value of a single-effect model (OWF only or CC only).

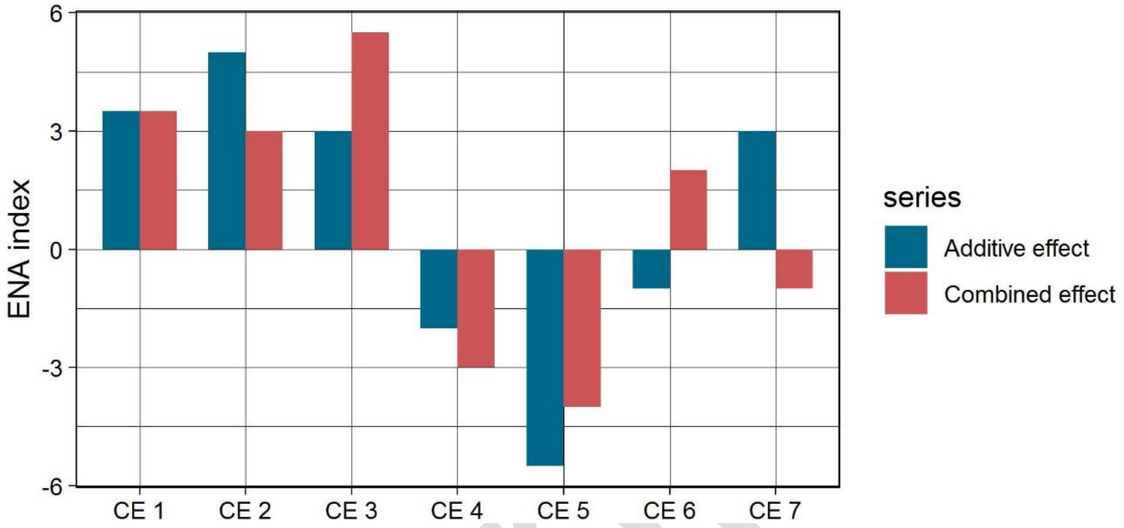


Figure - 3 A typology of potential cumulative effects (CE) resulting from the interactions of multiple drivers (Travers-Trolet et al., 2014***).***

Cumulative effects are determined by comparing the additive effect (sum of the individual effects of each driver; in blue) to the combined effect of both driver (in red). CE 1 is additive with no driver interactions; CE 2 is positive dampened; CE 3 is positive synergistic; CE 4 is negative synergistic; CE 5 is negative dampened; CE 6 is positive antagonistic; CE 7 is negative antagonistic.

3 Results

The ES supply indicators were mapped for the eBoS and show a higher supply for all indicators in the most coastal part of the study area, i.e. the Coastal Seine Bay (CBoS). We observe a decreasing intensity of the supply of all three ES, following a gradient from the coast to the open sea (Figure - 44). Indices either reflect the primary production map (regulation service, see Supplementary materials Figure S - 2), the depth map (cultural service, see Supplementary materials Figure S - 1), or follow a close coast to shore gradient (provisioning service). This demonstrates the relationship between the ecosystem and the environment defined in Ecospace using environmental drivers.

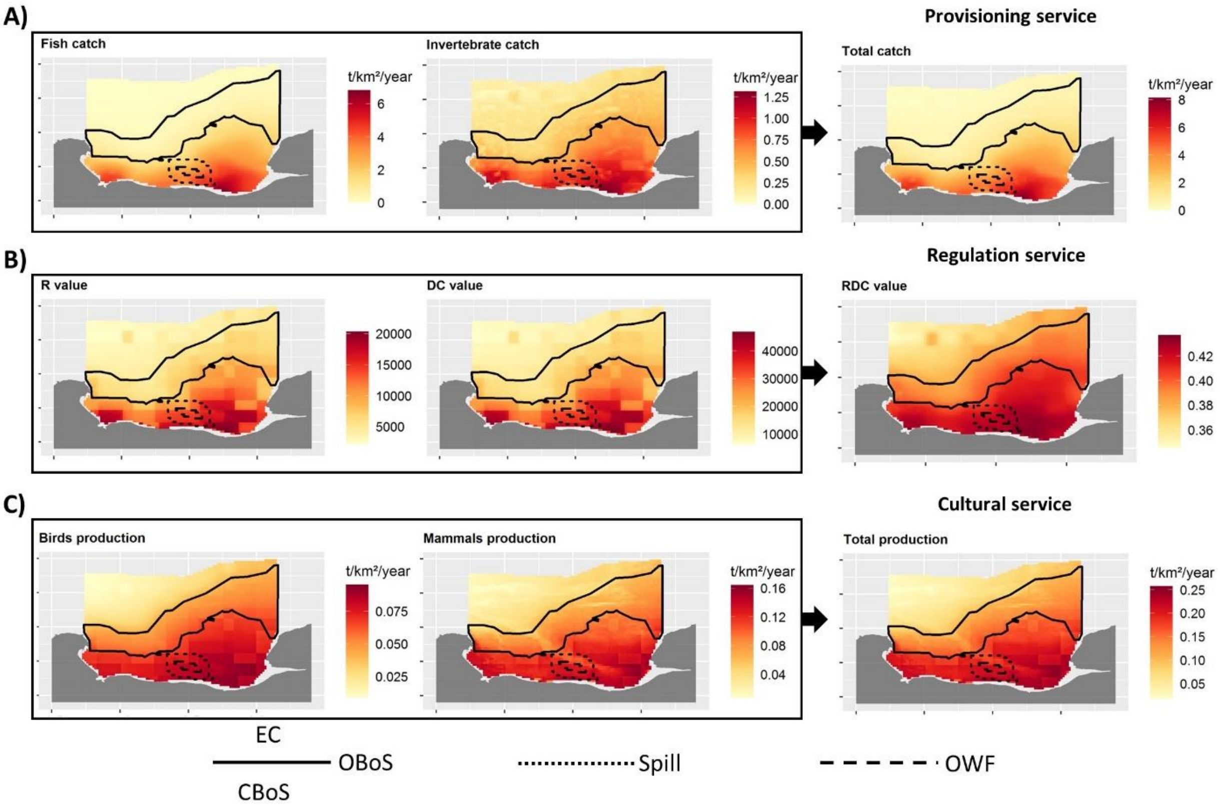
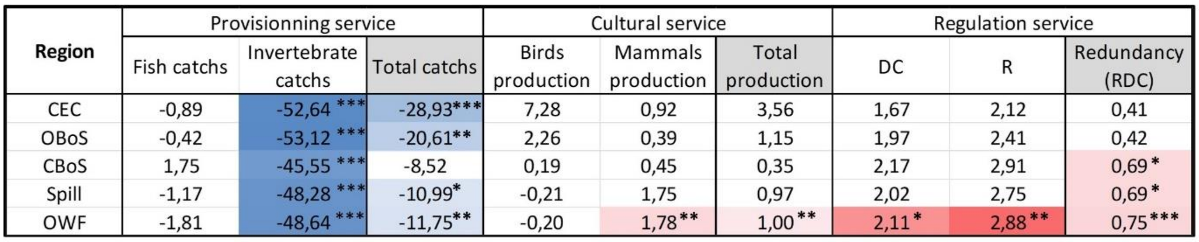


Figure - 4 Indicators of Ecosystem services supply in the extended Bay of Seine model.

The first two columns of maps present the components used to build the ES indices (third column). The regions and sub-regions of the model are also mapped with the dotted line mapping the OWF, the dotted one the spillover region and the continuous line each functional region of the eBoS (CBoS, OBoS, CEC).

For the effect of CC on the ES supply, the provisioning ES (total catch) seems to be the most impacted with around 30 % loss in the CEC region to approximately 9 % in the Coastal Bay of Seine region (Figure - 5). This appeared to be mainly linked to the loss of invertebrate catches while fish catches did not display any major evolution due to CC. The eBoS, invertebrate catches are mainly represented by King scallop catches (79% in the reference and 85% in the CC scenario). The other ES supplies are less impacted, but we notice an increase in the regulating ES for the most coastal region, with high local increase in resilience (RDC) as visible in the OWF sub-region. Finally, the cultural ES present limited changes due to CC, with very localized increase spotted in the OWF sub-region (Figure - 5).

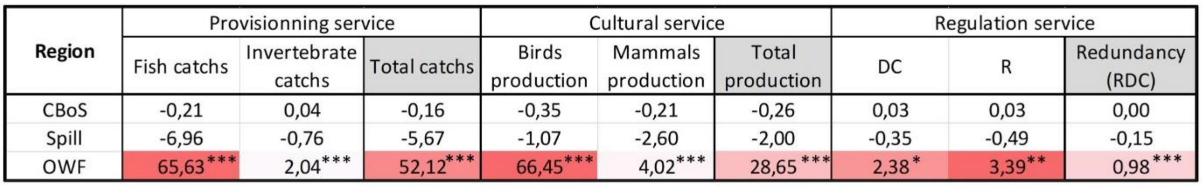


Region	Provisionning service			Cultural service			Regulation service		
	Fish catchs	Invertebrate catchs	Total catchs	Birds production	Mammals production	Total production	DC	R	Redundancy (RDC)
CEC	-0,89	-52,64 ***	-28,93***	7,28	0,92	3,56	1,67	2,12	0,41
OBoS	-0,42	-53,12 ***	-20,61**	2,26	0,39	1,15	1,97	2,41	0,42
CBoS	1,75	-45,55 ***	-8,52	0,19	0,45	0,35	2,17	2,91	0,69 *
Spill	-1,17	-48,28 ***	-10,99*	-0,21	1,75	0,97	2,02	2,75	0,69 *
OWF	-1,81	-48,64 ***	-11,75**	-0,20	1,78 **	1,00 **	2,11 *	2,88 **	0,75***

Figure - 5 Climate change effects in 2050 on the ecosystem services supply indicators compare to the reference scenario (in percent), per region.

Effects of CC were computed per functional and structural regions of the eBoS. To determine if the effect is important or not, Cliff's deltas were realized with variation considered: *** strong (| ∂Cliff | > 0.474); ** medium (0.33 < | ∂Cliff | < 0.474); * small (0.147 < | ∂Cliff | < 0.33); nothing, negligible (| ∂Cliff | < 0.147), ((Romano et al., 2006). Colors were plotted only on the indicators with a | ∂Cliff | > 0.147 and show the decreasing (blue) and increasing intensity (red) of the indices. Regions include: the Central English Channel (CEC), the Offshore Bay of Seine (OBoS) and the Coastal Bay of Seine (CBoS).

The potential reserve and reef effects of the future OWF of Courseulles-sur-Mer have strong impacts on the ES supply inside the park (Figure - 6). All the ES are affected, with large variations compared to the reference scenario: both the reserve and reef effects of the OWF appear to increase ES supply.



Region	Provisionning service			Cultural service			Regulation service		
	Fish catchs	Invertebrate catchs	Total catchs	Birds production	Mammals production	Total production	DC	R	Redundancy (RDC)
CBoS	-0,21	0,04	-0,16	-0,35	-0,21	-0,26	0,03	0,03	0,00
Spill	-6,96	-0,76	-5,67	-1,07	-2,60	-2,00	-0,35	-0,49	-0,15
OWF	65,63***	2,04***	52,12***	66,45***	4,02***	28,65 ***	2,38*	3,39**	0,98 ***

Figure - 6 Offshore wind farm effects on the ecosystem services supply indicators compare to the reference scenario (in percent), per region.

Effects of the OWF were computed per functional and structural regions of the eBoS. To determine if the effect is important or not, Cliff's deltas were realized with variation considered: *** strong (| ∂Cliff | > 0.474); ** medium (0.33 < | ∂Cliff | < 0.474); * small (0.147 < | ∂Cliff | < 0.33); nothing, negligible (| ∂Cliff | < 0.147), (Romano et al., 2006). Colors were plotted only on the indicators with a | ∂Cliff | > 0.147 and show the decreasing (blue) and increasing intensity (red) of the indices. Regions include: the Central English Channel (CEC), the Offshore Bay of Seine (OBoS) and the Coastal Bay of Seine (CBoS).

When both anthropogenic drivers are combined, cumulative effects appear near the OWF (Figure – 77). Despite the high variability of catches inside the OWF sub-region due to the partial reserve effect being applied for 6 of the 37 Ecospace cells of the park, visible on error bars (the same in both the separated and combined effects scenarios), a positive dampened effect can be seen on the provisioning ES supply in the OWF. The regulating ES had cumulative effects, but unlike the provisioning one, it is not only limited to the OWF since a small cumulative effect is also visible in the spillover region of the OWF, resulting in a positive synergistic effect. Inside the OWF, the regulating ES also experienced a positive dampened effect, like the provisioning ES. Finally, the cultural ES showed a positive synergistic effect of the combined CC and reef and partial reserve effects inside the OWF (Figure – 77).

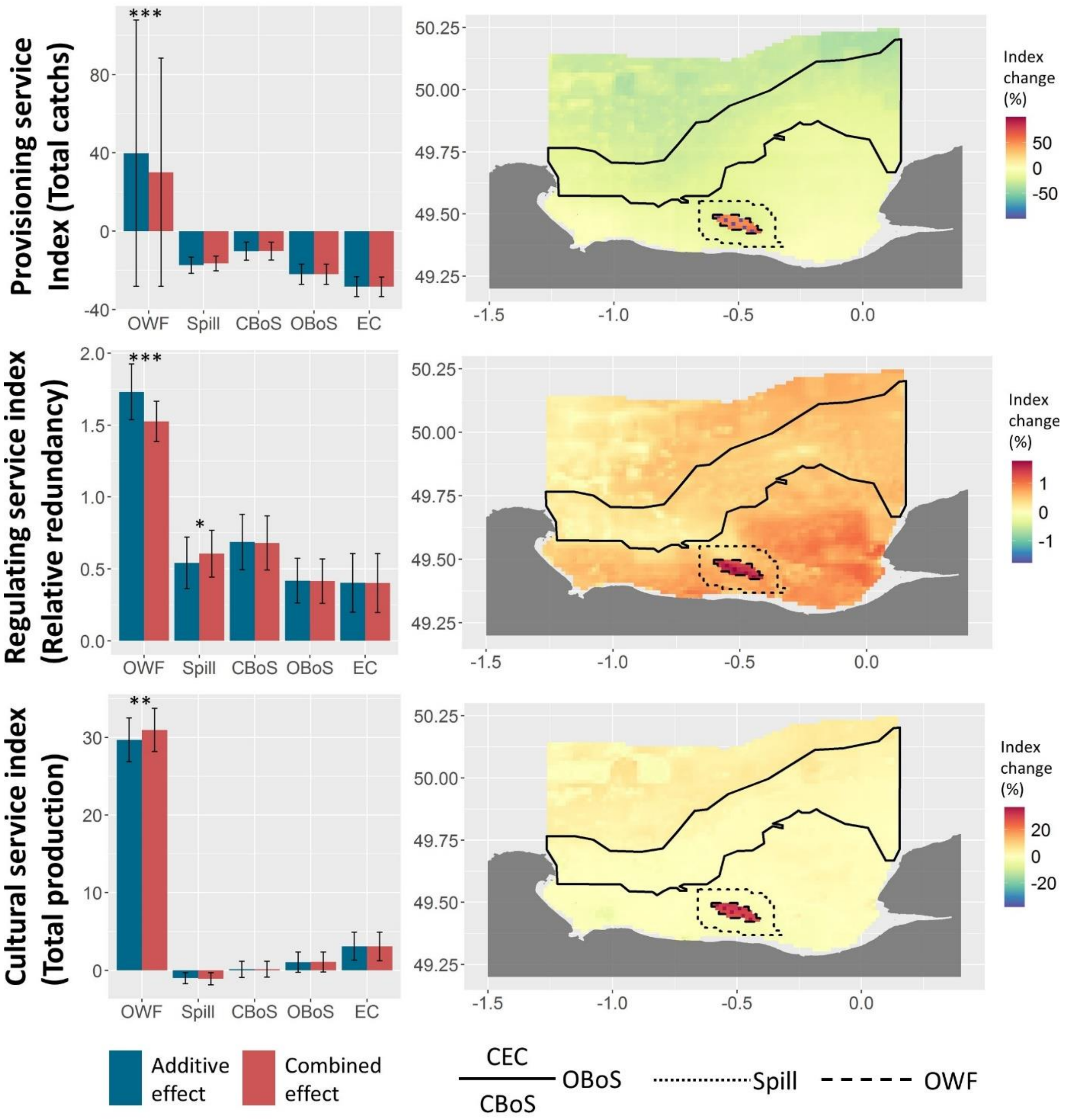


Figure – 7 Cumulative effects of climate change and of the offshore wind farm on the ecosystem services supply indices.

Bar charts compare the additive effects to the combined effects of both CC and of the OWF while the map plot combine the effects of both drivers on each ES supply indicators. Error bars display the standard deviation. To determine if cumulative effects were considered important or not, Cliff's deltas were realized with variation considered: *** strong (| ∂Cliff | > 0.474); ** medium (0.33 < | ∂Cliff | < 0.474); * small (0.147 < | ∂Cliff | < 0.33); nothing, negligible (| ∂Cliff | < 0.147).

4 Discussion

To our knowledge, this study constitutes the first attempt to quantify the supply of ES using ecological network analysis, through both holistic and functional indices. It aims to display the potential and usefulness of food web models in the ES framework. However, this comes with limitations that are worth to be kept in mind. They come from the wide range of CC effects or OWF effects. One can hardly model the full extent of these effects, especially since they are still under debate amongst the scientific community (Dannheim et al., 2020). One way to tackle this issue is to better consider the uncertainty around the input of the model, either through the biological constraints (Meersche et al., 2009; Steenbeek et al., 2018), or through the forcing inputs like the suitability index maps computed by the niche models (Bourdaud et al., 2021). However, this was not done due to computation time but should be encouraged in future works. This does not prevent this study from identifying trends related to expected changes in the environment. Further, this paper is based on the previous studies of the eBoS that did not attempt to model the full extent of the effects of CC and the OWF but rather, to model their main and most structuring effects on the food web and then to gradually improve on them. We thus benefit from the improvements on the OWF simulation from Halouani et al. (2020) and on CC simulation from Bourdaud et al. (2021), while giving new insights compared to Nogues et al. 2022 on impacts for humans.

4.1 Climate change effect on the ecosystem services supply of the eBoS

Climate change appears to have a significant effect on ES supply. With losses reaching up to 30% for the supply of the provisioning ES, CC seems to have a major impact on the food production of the eBoS. This appears to be mainly due to losses in invertebrate catches, attributed to the important decrease of King Scallops (*Pectens maximus*) suitability, which play a major part in invertebrate catches. This potentially high impact of CC on this species of shellfish was already pointed out in (Lavaud, 2014; Rombouts et al., 2012). This would result from the expected Northward drift of many cold-water species due to the expected increase in water temperature (Kleisner et al., 2017, 2016; Nye et al., 2009). While a similar decrease in king scallop catches was also observed in Bourdaud et al. (2020), here it is the result of a decrease in environmental suitability rather than a shift within the bay (different methodology to model climate change). In Bourdaud et al. (2020), catches of other species like Atlantic cod were also negatively impacted by CC in 2100, while in this case, in 2050, only king scallop catches were significantly affected.

Fishing, in particular King scallop fishing, plays a key economic role in Normandy. King scallop represents ~40% of the seafood sales at the Port-en-Bessin fish market (Buléon and Shurmer-Smith, 2021), making it one of the most valuable species in the eBoS. The evolving supply of the food provisioning ES, linked to the changing rate between fish and invertebrate capture due to CC will thus have a major impact on fishing fleets which will necessarily have to evolve. In a political context (Brexit) where the areas and quotas dedicated to fishing are already restricted and with the recent effects of the Covid-19, one can only assume that CC will have a major effect on Normandy economy and socio-cultural fabric. The whole fishing sector (fishmongers, shipyards, fish processing industries) may not be able to resist to such an evolution. Fishing (in particular king scallop fishing) also plays an essential part in tourism industry, including local gastronomy and restaurants, reflecting a strong synergy between the food 21rovisioning ES and the cultural Ess. Potential changes in the stocks of king scallops could then have economic and socio-cultural repercussions far beyond the frame of the Seine Bay fishery and affecting many beneficiaries. The indicator of the supply of the food 21rovisioning ES could then reflect change in several Ess and components of the social system (Haraldsson et al., 2020; Niquil et al., 2021), caused by CC. Here, the provisioning indicator is thus more akin to a link between two different systems, the ecological system and the social system that depends on fishing and king scallops the social and the ecological system, where one perturbation in the ecosystem can cascade throughout the social system (Haraldsson et al., 2020; Niquil et al., 2021). CC could also impact fish quality and availability, but we didn’t consider such aspects in this study (Bourdaud et al., 2021; Pauly et al., 1998).

The effects of climate change on ES supply are not all negative. One potentially light positive effect of CC on the eBoS is the possible increase in the ecological resilience of the food web. This is visible as the supply of the regulating ES increases in the coastal zone of the eBoS. While small, the increase remains significative and can indicates important changes in the ecosystem organization and functioning (e.g. Tomczak et al. 2013). This effect is however very specific to this system and cannot be generalized for other systems as it depends on the organization and functioning of the initial system. Climate change modeling is subject to many uncertainties, and many more effects might arise from it (Harley et al., 2006; Wernberg et al., 2012). However, this shows potential tradeoff in the effects of anthropogenic drivers on ES supply. With CC having potentially important negative effects on part of the ecosystem, resulting in the hypothetic decrease of the supply of one service (food provision), but not on the hole system and thus on other services supply. Food web models thus show their ability in describing the functional mechanisms at the root of tradeoff, required for spatial planning in ecosystem management (Aryal et al., 2022).

4.2 Offshore wind farm effect on ecosystem services supply in the eBoS

The OWF of Courseulles-sur-Mer reef and partial reserve effects seem to have a positive effect on the ES supply in the eBoS, for all the studied ES supply indicators. This finding confirms the results obtained in several previous studies that showed that not only fishermen could benefit of the OWF despite losses in fishing areas (Halouani et al., 2020) but the OWF also has a positive effect on the food web resilience (Raoux et al., 2019).

One of these positive effects is the increased production of flagship species due to the reef and partial reserve effects of OWF. This impacts species like marine mammals such as bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*), and surface feeding sea birds like gulls (*Larus sp*). Studies have already shown positive effects of the OWF on these species, with some displaying an attractive effect of wind turbines on some marine seabird like gulls (Blew et al., 2008; Vanermen et al., 2015), while other have described a similar attraction of marine mammals like harbour porpoises (Scheidat et al., 2011) or no effects at all on grey and harbor seals (Edrén et al., 2010; Tougaard et al., 2006).This must however be taken carefully. Indeed, one of the limitations of our approach is that the OWF effect on the ecosystem was limited to the expected main effects of the OWF on the ecosystem i.e. the underwater reef and partial reserve effects. However, the OWF can have other important effects that may not be as structuring. On one hand, several studies have pointed out the potential negative effects of OWFs on such species like the dislocation or collision effects of OWF on seabird species like northern gannets (Blew et al., 2008; Furness et al., 2013; Vanermen et al., 2019) or on migratory species (Masden et al., 2009), as well as the potential effects of underwater noise of wind turbines on marine mammals like harbour porpoises feeding behavior (Carstensen et al., 2006). However, some pointed out the potential adaptive power of marine mammals to environmental changes, which may limit the negative effects of the OWF (Tyack, 2008). Here, we can say that the modelled effects of the

OWF of Courseulles-sur-Mer may benefit flagship species by increasing their prey densities in the OWF (Lindeboom et al., 2011), as visible in the strong increase of fish capture inside the OWF. The increase in marine mammals' preys like whiting (*Merlangius merlangus*) and pouting (*Trisopterus luscus*) is straight forward as they are directly benefiting from the reef effect on smaller benthic invertebrates like invertebrate filter feeders. For sea birds on the other, this is explained by the increase in the production of prey species not directly benefiting from the reef effect of the OWF like European sprat (*Sprattus sprattus*) and European pilchard (*Sardina pilchardus,* see supplementary materials Figure S – 3 & 4 and Table S - 8 & S2 - 2). Rather, these species benefited from the indirect effect of the OWF on the hole ecosystem, only observable when considering the entire food web.

4.3 The combined effects of both drivers

Combining the effects of the OWF and of CC resulted in significant cumulative effects (CE) on each indicator of ES supply. The OWF seems able to limit the losses of the provisioning ES caused by CC, while improving the supply of the cultural and the regulating ones. This is mainly visible inside the OWF, where driver interactions were the strongest. The interactions between the drivers resulted in CE (difference between the additive and the cumulative effects), but with different ranges between the indicators. As such the ENA index showed small CE around the OWF, in the spillover region, while the community-based indicators (catches, and flagship species productions), mainly display CE within the farm. These observations go alongside previous works indicating that CE happen often when two or more drivers interact with each other (Darling and Côté, 2008); and that the spatial extent of cumulative effects can vary depending on the studied ecosystem property, with some CE able to happen outside of the expected zone of anthropogenic driver's interaction (Nogues et al., submitted). Marine protected areas and artificial reefs have already demonstrated their ability to increase ES supply (Leenhardt et al., 2015; Qin et al., 2011; Ramos et al., 2019). We demonstrate that, in Courseulles-sur-Mer, the reef and partial reserve effects seem to be able to keep this ability to increase ES supply, despite the effect of climate change. This is in spite of the dampening CE resulting from both drivers' interaction, visible with the lower increase in ES supply in the combined effect compared to the additive one (see Figure - 7). As the positive reef and partial reserve effects remain limited in space, this could emphasize the need for ecological management plans at a larger spatial scale (Charles, 2012), as to prevent the impact of CC on ES supply and thus on human wellbeing.

4.4 Spatial planning using food web models

Ecosystem approaches like food web models can also inform marine planification by identifying key areas for ES supply. The link between ES supply indicators being strongly associated to ecological and trophic mechanism, as species interact with other species within their vicinity (depending on their ability to move), specific ecological areas are going to stand out. In the Bay, the coastal region is the most productive and the most diverse ecologically. This increase the odds that this area of the ecosystem is going to play a key role in ES supply (Sieber et al., 2018). This is evident from the higher value of the ES supply indices in the coastal area of the bay. This could thus justify management action to maintain ES supply, like a three-mile coastal zone of restricted fishing activities like trawling (Engel and Kvitek, 1998; Pranovi et al., 2015). Another possible path could be to benefit ES supply in more offshore areas of the bay, where the supply of ES is lesser. With the reef and reserve effect of the OWF increasing ES supply, these offshore areas could be selected for future OWF installations, which could not only benefit the studied ES supply, but could also limit the aesthetical impact on the landscape (Sullivan et al., 2013), despite the increased cost of more offshore farms (Virtanen et al., 2022).

Coastal regions are sensitive environments, subject to a high concentration of human activities (He and Silliman, 2019) highly vulnerable to environmental change (eutrophication or global warming). This makes the mapping of ES supply crucial for management as it gives insight about the importance of these areas for humans (Maes et al., 2012), as seen here. Using ecosystem approaches to support management could allow for a better forecasting of these impacts on the ecosystem and the ability to explore new solutions, making food web model invaluable for managing coastal ecosystem.

4.5 Food web model: toward a more ecosystem-based approach of ecosystem services

Integrative and connected approaches are lacking in ES studies (García-Onetti et al., 2018). The proxies most often used to map the supply of marine ES are bathymetric maps, habitat distribution maps, sediment maps, tidal maps and water temperature maps (Lavorel et al., 2017). However, these parameters do not consider the interconnectivity of marine systems and are not sufficient to characterize the supply of marine ES (Dee et al., 2017; Guerry et al., 2012). Moreover, ES relations in space and time are in general defined using correlative approaches (Agudelo et al., 2020; Lee and Lautenbach, 2016; Li et al., 2018), without any information on causal mechanisms responsible for these relationships.

To identify tradeoff between ES, methodological advances need to be made to quantify how relationships between species / ecological functions shape the supply of ES. Ecological functions such as primary production or secondary production, play a key role in supplying ES (Armoškaitė et al., 2020; Martinetto et al., 2020). However, through the increasing subdivision of ES and of the ecological functions they are relying on (Hummel et al., 2019), one may consider processes as disconnected. In nature, these functions are all interconnected, forming a continuum between species/groups - functions and ES. The quantification of ES needs to take this connectivity into account (De Groot et al., 2010), as it enables:

- The detection of causal relationship between ES. Such relationship can be linked to a species playing a role in the supply of multiple services (Duncan et al., 2015). This shown here with the effects of the OWF on demersal and benthic fish like poutings (*Trisopterus luscus*), dragonets (*Callionymidae sp*), cods (*Gadus morhua*) and various flat fishes (Supplementary materials Table S - 10) in the bay. With the increase of fish production and biomass due to the OWF, captures increase within the OWF, which benefits the provisioning ES. However, this will also benefit flagship species like marine mammals which will have more available food, increasing the supply of the cultural ES (Busch et al., 2010). Relationships can also be based on other vectors like fishing discards. Indeed, the increase in catches inside the OWF resulted in a higher amount of discards, benefiting surface feeding seabirds like gulls, which are known to feed from it (Montevecchi, 2001; Garthe and Scherp, 2003; Karris et al., 2018). With the increase of catches and the increase in flagship species production within the OWF like Gulls, there is therefore no tradeoff between the cultural and provisioning ES despite both potentially competing for the same resources.
- The Quantification of new types of ES, such as services depending on the organisation of the food web (e.g. ecosystem resilience - Contanza, R and Mageau,

1999; Saint-Béat et al., 2015) and thus on the overall functioning of the ecosystem (Kremen 2005). For example, the increase in the production of some fish groups like pouting due to the OWF will not only benefit the provisioning service since it is fished or the cultural service since it is a prey to marine mammals like dolphins, but it will also, in part, increase the redundancy of trophic pathways, improving the ecosystem resilience.

These benefits open ways to study a wider range of ES, with better forecasting power (De Groot et al., 2010; Müller et al., 2010). For example, the cultural ES category has often been back sided (Blicharska et al., 2017). Such an omission may be explained by the oversimplification of the attachment of humans to the natural world and the fracture in sciences between nature and culture. Like ecosystems and their role in ES supply, the cultural construct is directly related to the ecosystem functioning and organization, intertwined through multiple species, functions and ES, rather than compartmentalized (Mongruel et al., 2019). For example, food production has fostered development of rich fishing cultures, that vary by location, in terms of fished species but also of local communities, boats and other technologies, physical port characteristics, fish markets, and, obviously, culinary practices. The present study has shown a potential collapse of scallop populations under CC effects. If the consequences on the provisioning ES are clear, it will also have repercussions on the whole social system since scallop fishing in a way shapes the coastal Normandy's identity. Strong link between cultural and other categories of ES are revealed here, which are often underestimated (Blicharska et al., 2017). These inter-woven relationships have been described and studied in Humanities and Social sciences and should be further integrated in ES studies.

Conclusion

This study demonstrates that food web models are useful for mapping, quantifying, and understanding the mechanism of ES supply and its evolution in the face of environmental changes. It determined that the coastal part of the bay of seine played a key role in ES supply, making this area a priority for conservation. Our model revealed that OWF could increase the studied ES supply, it also described the multi-species mechanisms responsible for such increase. It showed that CC was going to have significant effect on some ES, with potentially strong repercussion for the social system. Despite this, and the potential cumulative effects with CC, the OWF was still able to limit locally some of the effects of CC.

The food web model utilized here was also able to detect links between ES, based on a posteriori observations and analysis, determining specific tradeoff between ES supply. This was possible since food web model look at what makes ecosystems unique: species living in it and the relationships between them, instead of making correlations based on previously observed relationships in other unrelated systems. Food web models also allow the mobilization of ecological theories rarely employed within the ES framework. Indeed, ES supply is often quantified using observations and non-mechanistic approaches (coverage areas, fishing values… Dade et al. (2019)). However, such structural information can hardly characterize the functioning of ecosystems and the complex mechanisms at work within them. Food web models and ecological network analysis thus gives new insights on previously poorly mobilized information. Finally, food web models such as Ecospace enable the mapping of ES supply while accounting for complex ecological mechanisms such as species movement, habitat suitability and species interactions, providing a better mapping of ES and a higher predictive potential.

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Competing interest statement

The authors have no conflict of interest to declare.

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Supplementary materials

Table S - 1: Previous modeling works on the extended Seine Bay.

Sources	Models	Objectives	Description and additions
Raoux et al. 2017	EwE: Ecopath steady state model	- Study of the Courseulles-sur-Mer offshore wind farm (OWF) effects on the local food web. - Trophic network analysis of the consequences of the OWF for the ecosystem structure and functioning.	- Ecopath modeling of the Courseulles-sur-Mer food web before and after the construction of the offshore wind farm. - Model the impact of additional hard substrates (reef effect), and fishing closure (reserve effect) on the local food web.
Halouani et al. 2018	EwE: Ecopath, Ecosim and Ecospace steady state and dynamic models	- Spatial study of the extended Seine Bay (eBoS). - Sensitivity analysis of fishing closure inside the Courseulles-sur-Mer OWF for fisheries in the Seine Bay.	- Ecopath update over Raoux et al. 2017. - Ecosim and Ecospace dynamic model setup. - Ecospace set up using habitat parameters based on depth and sediment types.
Ben Rais Lasram et al. 2019	Species distribution models (not EwE)	Development of a multi-algorithms and hierarchical species distribution modeling method used on species endemic to the Seine Bay.	- Hierarchical method using both climatic and habitat parameters to model a wide range of species distribution and their evolution due to climate change.
Bourdaud et al. 2020	EwE: Ecosim and Ecospace dynamic models	- Study the potential effects of climate change on species distribution on the Seine Bay food web. - Consequences of CC for fisheries.	- Integrates species displacement linked to CC in Ecospace using SDMs outputs, to consider the effect of predators-preys relationships.
Nogues et al. 2022	EwE: Ecospace dynamic models	- Study of the effects of multiple anthropogenic drivers on the Seine Bay ecosystem functioning. - Modeling of climate change, the OWF reef and full reserve effects, and potential effects of Brexit on fishing. - Spatial assessment of the ecosystem functioning using spatial ecological network analysis.	- Uses SDMs outputs to characterize habitat suitability modifications due to climate change on multiple species. - Adds the partial reserve effect and the reef effect of the OWF of Courseulles-sur-Mer in Ecospace. - Models various fishing efforts scenarios. - Uses spatial ecological network analysis to map ecosystem properties and functioning.

1219 ***Table S - 2: Input data used in each modelling approach.***

Models	Origins	Input types	Targets	Sources
Ecopath	Raoux et al. 2017; Halouani et al. 2018	Groups biomass, production, consumption, ecotrophic efficiency and diet.	All groups	See Raoux et al. 2017 and Halouani et al. 2018 for details
Ecosim	Halouani et al. 2018	Primary production forcing time series	Phytoplankton	- Satellite ocean data (SeaWifs): (NASA Goddard Space Flight Center and Ocean Biology Processing Group, 2014 - Satellite ocean data (MODIS): Hu et al., 2012
Ecosim	Halouani et al. 2018	Catches, biomass, and fishing mortality time series (for calibration, 29 total)	Fished groups, for the complete list see Halouani et al. 2018.	- SACROIS data (Système d'Information Halieutique, 2017) - Stock assessment data from COMOR campaign report (Foucher, 2013) - Estimated from a surplus-production model (SPiCT) (Pedersen and Berg, 2017) see Halouani et al 2018
Ecosim	Halouani et al. 2018	Fishing efforts time series (1 per fleet)	Fishing fleets	SACROIS data (Système d'Information Halieutique, 2017)
Ecospace	Halouani et al. 2018	Primary production forcing map	Phytoplankton	SeaWifs Chlorophyll a map (https://podaac.jpl.nasa.gov/)
Ecospace	Halouani et al. 2018	Depth forcing map	Depth driven species (see table s - 5)	GEBCO (General Bathymetric Chart of the Oceans: https://www.gebco.net/)
Ecospace	Halouani et al. 2018	Depth forcing functions	Depth driven species (see table s - 5)	See Halouani et al. 2018
Ecospace	Bourdaud et al. 2021; Nogues et al. 2022	Environmental suitability maps (27 total)	Environmental driven species (see table s - 5)	Maps built from Lasram Ben Rais et al. (2019) SDM approach using World Ocean Atlas 2013 V2 historical climatic parameters (https://www.ncei.noaa.gov/products/ocean-climate-laboratory), EMODnet habitat parameters (https://emodnet.ec.europa.eu/en) and various species occurrences data (see Table S - 3)
Ecospace	Nogues et al. 2022	Environmental suitability forcing function	Environmental driven species (see table s - 5)	See Nogues et al. 2022

Ecospace	Nogues et al. 2022	Offshore wind farm suitability maps	Species impacted by the reef effect (see table s - 5)	Maps built from Raoux et al. 2017, see Nogues et al. 2022
Ecospace	Nogues et al. 2022	Offshore wind farm partial reserve map	Fished species	Maps built from Raoux et al. 2017 and Halouani et al. 2018, see Nogues et al. 2022

Table S - 3: Species distribution model inputs

Model type	Group	Data type	Sources
Climatic (global)	All	Sea surface temperature and salinity (first 50 meters), intermediate sea temperature and salinity (50-200 meters), bottom sea temperature and salinity (last 50 meters)	World Ocean Atlas 2013 V2 historical climatic parameters (https://www.ncei.noaa.gov/products/ocean-climate-laboratory)
Habitat (local)	Benthic and demersal groups	Type of substrate, bathymetry, slope and the orientation of the slope towards the north.	EMODnet-bathymetry (http://www.emodnet-bathymetry.eu/) and EMODnet- seabedhabitats (http://www.emodnet-seabedhabitats.eu/).
All	All	Species occurrences	- Global: OBIS (Ocean Biogeographic Information System); GBIF (Global Biodiversity Information Facility); iNaturalist (A Community for Naturalists); VertNet (vertebrate biodiversity networks); Ecoengine (UC Berkeley's Natural History Data) - Local: IBTS (International Bottom Trawl Survey), CGFS (Channel Ground Fish Survey), EVHOE (Evaluation Halieutique Ouest de l'Europe), CAMANOC and various M2C missions.

Table S - 4 Ecological groups of the extended bay of Seine Ecospace model with their species composition Fished groups are in grey (light grey: invertebrates, dark grey: fish). Flagship species are in green (light green: marine mammals, dark green: Seabirds).

Ecopath functional group	Species composition
Fish Limande	*Limanda limanda*
Fish Flounder	*Platichthys flesus*
Fish european plaice	*Pleuronectes platessa*
Fish sole	*Solea solea*
Fish sea bream	*Spondyliosoma cantharus*
Fish benthos feeders	*Callionymus*
	Mullus surmuletus
	Labrus bergylta
	Zeus faber
Fish planctivorous	*Clupea harengus*
	Engraulis encrasicolus
Fish piscivorous	*Pollachius pollachius*
Fish european sprat	*Sprattus sprattus*
Fish european pilchard	*Sardina pilchardus*
Fish poor cod	*Trisopterus minutus*
Fish pouting	*Trisopterus luscus*
Fish gurnard	*Chelidonichthys lucerna*
	Chelidonichthys lastoviza
Fish atlantic horse mackerel	*Trachurus trachurus*
Fish whiting	*Merlangius merlangus*
Fish atlantic cod	*Gadus morhua*
Fish sharks	*Mustelus mustelus*
	Scyliorhinus canicula
	Scyliorhinus stellaris
Fish rays	*Raja clavata*
	Raja montagui
Fish european seabass	*Dicentrarchus labrax*
Fish mackerel	*Scomber scombrus*
Benthic cephalopods	*Sepia officinalis*
Benthopelagic cephalopods	*Alloteuthis spp*
	Loligo vulgaris
Surface feeders seabirds	*Larus argentatus / Larus michahellis / Larus marinus / Larus fuscus*
	Larus sp
	Larus ridibundus/ Larus melanocephalus
	Rissa tridactyla
	Sterna paradisaea/ Sterna hirundo/ Sterna albifrons/ Thalasseus sandvicensis
Plunge and pursuit divers' seabirds	*Fratercula arctica / Uria aalge / Alca torda*
	Morus bassanus
	Gavia stellata/ Gavia arctica/ Gavia immer
	Phalacrocorax carbo / Phalacrocorax aristotelis
	Fulmarus glacialis
Benthic feeders seabirds	*Melanitta nigra / Melanitta fusca*
Phocidae	*Halichoerus grypus*
	Phoca vitulina
Harbour porpoises	*Phocoena phocoena*

Ecopath functional group	Species composition
Bottlenose dolphins	*Tursiops truncatus*
King scallops	*Pecten maximus*
Benthic inv bivalves filter feeders	*Acanthocardia echinata*
	Angulus fabula
	Angulus pygmaeus
	Corbula gibba
	Ensis
	Ensis directus
	Ensis magnus
	Kurtiella bidentata
	Lanice conchilega
	Lutraria lutraria
	Mactra stultorum
	Moerella donacina
	Parvicardium scabrum
	Phaxas pellucidus
	Spisula elliptica
	Spisula subtruncata
	Tellimya ferruginosa
	Thracia phaseolina
Benthic inv deposit feeders (Subsurface)	*Amphilochus neapolitanus*
	Aphelochaeta marioni
	Bathyporeia
	Bathyporeia elegans
	Bathyporeia guilliamsoniana
	Bathyporeia tenuipes
	Capitella capitata
	Capitella minima
	Capitellidae
	Caulleriella alata
	Caulleriella viridis
	Caulleriella zetlandica
	Chaetozone christiei
	Chaetozone gibber
	Chaetozone setosa
	Echinocardium cordatum
	Notomastus latericeus
	Nucula hanleyi
	Nucula nitidosa
	Phascolion (Phascolion) strombus strombus
	Scalibregma inflatum
	Scoloplos (Scoloplos) armiger
	Spio decoratus
	Spiophanes bombyx
	Abludomelita obtusata

Ecopath functional group	Species composition
Benthic inv deposit feeders (Surface)	*Abra alba*
	Acrocnida brachiata
	Ampharete baltica
	Amphicteis gunneri
	Amphipholis squamata
	Aonides oxycephala
	Aonides paucibranchiata
	Aora gracilis
	Apseudopsis latreillii
	Atylus vedlomensis
	Bodotria arenosa
	Bodotria pulchella
	Bodotria scorpioides
	Cheirocratus
	Cheirocratus intermedius
	Corophium
	Crassicorophium bonellii
	Diastylis bradyi
	Diastylis laevis
	Gastrosaccus sanctus
	Gastrosaccus spinifer
	Lagis koreni
	Magelona filiformis
	Magelona johnstoni
	Megaluropus agilis
	Megamphopus cornutus
	Melinna palmata
	Nebalia bipes
	Owenia fusiformis
	Pariambus typicus
	Perioculodes longimanus
	Phtisica marina
	Pinnotheres pisum
	Poecilochaetus serpens
	Polycirrus medusa
	Pontocrates arenarius
	Pseudocuma (Pseudocuma) longicorne
	Scolelepis (Scolelepis) squamata
	Scolelepis bonnieri
	Siphonoecetes (Centraloecetes) kroyeranus
	Synchelidium maculatum
	Urothoe elegans
	Urothoe poseidonis
Benthic inv filter feeders	*Ampelisca*
	Ampelisca brevicornis

Ecopath functional group	Species composition
	Ampelisca diadema
	Ampelisca spinipes
	Ampelisca tenuicornis
	Ampelisca typica
	Phoronis psammophila
	Pisidia longicornis
	Spirobranchus
	Thyone fusus
Benthic inv predators	*Antalis vulgaris*
	Asterias rubens
	Eteone longa
	Eualus cranchii
	Eulalia mustela
	Eumida
	Eumida bahusiensis
	Eumida sanguinea
	Eunereis longissima
	Eurydice pulchra
	Euspira pulchella
	Exogone (Parexogone) hebes
	Glycera gigantea
	Glycera lapidum
	Glycera tridactyla
	Glycinde nordmanni
	Haplostylus normani
	Harmothoe
	Harmothoe glabra
	Harmothoe pagenstecheri
	Malmgreniella arenicolae
	Myrianida
	Mysta picta
	Nemertea
	Nephtys assimilis
	Nephtys cirrosa
	Nephtys hombergii
	Nephtys kersivalensis
	Nymphon brevirostre
	Paranaitis kosteriensis
	Philocheras bispinosus bispinosus
	Pholoe baltica
	Phyllodoce
	Phyllodoce lineata
	Phyllodoce longipes
	Phyllodoce maculata
	Phyllodoce mucosa

Ecopath functional group	Species composition
	Phyllodoce rosea
	Processa edulis edulis
	Processa modica modica
	Protodorvillea kefersteini
	Sigalion mathildae
	Sthenelais boa
	Tubulanus polymorphus

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1228 ***Table S - 5 Trophic groups of the eBoS Ecopath with Ecosim model.***

Number of groups	Trophic groups	Environmental drivers
1	Phytoplankton	Primary production map
2	Bacteria	Everywhere
3	Microzooplankton	Everywhere
4	Mesozooplankton and macrozooplankton	Everywhere
5	Meiofauna	Everywhere
6	Suprabenthos	Everywhere
7	Benthic inv. deposit feeders (surface)	Suitability index map
8	Benthic inv. deposit feeders (subsurface)	Suitability index map
9	King scallop	Suitability index map
10	Benthic inv. bivalves filter feeders	Suitability index map
11	Benthic inv. filter feeders	Suitability index map
12	Benthic inv. predators	Suitability index map
13	Fish limande	Suitability index map
14	Fish flounder	Suitability index map
15	Fish European plaice	Suitability index map
16	Fish sole	Suitability index map
17	Fish sea bream	Suitability index map
18	Fish benthos feeders	Suitability index map
19	Fish planktivorous	Suitability index map
20	Fish piscivorous	Suitability index map
21	Fish European sprat	Suitability index map
22	Fish European pilchard	Suitability index map
23	Fish poor cod	Suitability index map
24	Fish pouting	Suitability index map
25	Fish gurnard	Suitability index map
26	Fish Atlantic horse mackerel	Suitability index map
27	Fish whiting	Suitability index map
28	Fish Atlantic cod	Suitability index map
29	Fish sharks	Suitability index map
30	Fish rays	Suitability index map
31	Fish European seabass	Suitability index map
32	Fish mackerel	Suitability index map
33	Benthic cephalopods	Suitability index map
34	Benthopelagic cephalopods	Suitability index map
35	Surface feeders sea birds	Everywhere

Number of groups	Trophic groups	Environmental drivers
36	Plunge and pursuit diverse sea birds	Everywhere
37	Benthic feeders sea birds	Depth dependent
38	Phocidae	Depth dependent
39	Harbor porpoises	Depth dependent
40	Bottlenose dolphins	Depth dependent
41	Discards	Everywhere
42	Detritus	Everywhere

Table S - 6 Fitted climatic species distribution models used to compute environmental driver maps for each trophic group of the eBoS Ecospace model. Models include: multiple regressions (Generalized Linear Model, Generalized Additive Model, Multiple Adaptive Regression Splines), regression trees (Boosted Regression Tree from GBM, Random Forest, Classification Tree Analysis), discriminant analysis (Flexible Discriminant Analysis) and learning techniques (Artificial Neural Network).

			climatic							
Ecopath trophic group	Latin name	Proportion in the group	MARS	ANN	CTA	FDA	GAM	GBM	GLM	RF
Benthic cephalopods	*Sepia officinalis*	1.00	1		1		1	1	1	1
Benthic inv. deposit feeders (Subsurface)	*Echinocardium cordatum*	0.66	1		1	1	1	1	1	1
Benthic inv. deposit feeders (Surface)	*Ophiothrix fragilis*	0.45	1		1	1		1	1	1
Benthic inv. deposit feeders (Surface)	*Pectinaria koreni*	0.15	1			1			1	
Benthic inv. filter feeders	*Psammechinus miliaris*	0.15	1		1			1		1
Benthic inv. predators	*Asterias rubens*	0.03	1	1		1	1		1	1
Benthic inv. predators	*Buccinum undatum*	0.11							1	
Benthic inv. predators	*Owenia fusiformis*	0.66								
Benthic inv. predators	*Sagartia troglodytes*	0.09					1			
Benthopelagic cephalopods	*Alloteuthis subulata*	0.09			1	1			1	
Benthopelagic cephalopods	*Loligo vulgaris*	0.91	1				1	1	1	1
Benthic inv. bivalvia filter feeders	*Aequipecten opercularis*	0.02	1			1	1	1	1	1
Benthic inv. bivalvia filter feeders	*Ensis directus*	0.00	1		1	1	1	1	1	1
Benthic inv. bivalvia filter feeders	*Glycymeris glycymeris*	0.61			1	1			1	1
Benthic inv. bivalvia filter feeders	*Lanice conchilega*	0.01	1	1	1	1	1	1	1	1

Fish Atlantic cod	*Gadus morhua*	1.00	1	1		1	1	1	1	1
Fish dab	*Limanda limanda*	1.00	1			1	1	1	1	1
Fish benthos feeders	*Callionymus lyra*	0.48	1			1	1	1	1	1
Fish benthos feeders	*Labrus bergylta*	0.07	1		1	1	1	1	1	1
Fish benthos feeders	*Mullus surmuletus*	0.27				1		1	1	1
Fish benthos feeders	*Zeus faber*	0.18	1		1	1	1	1	1	
Fish piscivorous	*Pollachius pollachius*	1.00	1		1	1	1	1	1	1
Fish planktivorous	*Clupea harengus*	0.91	1		1	1	1	1	1	1
Fish planktivorous	*Engraulis encrasicolus*	0.09	1	1	1		1	1	1	1
Fish flounder	*Platichthys flesus*	1.00	1		1	1	1		1	1
Fish gurnard	*Chelidonichthys lastoviza*	0.30	1		1	1	1	1	1	1
Fish gurnard	*Chelidonichthys lucerna*	0.70	1			1	1		1	1
Fish Atlantic horse mackerel	*Trachurus trachurus*	1.00	1		1	1	1	1	1	1
King scallop	*Pecten maximus*	1.00	1			1			1	
Fish mackerel	*Scomber scombrus*	1.00	1				1		1	1
Fish pilchard	*Sardina pilchardus*	1.00	1		1		1		1	1
Fish plaice	*Pleuronectes platessa*	1.00	1			1	1		1	1
Fish poor cod	*Trisopterus minutus*	1.00	1			1	1		1	
Fish pouting	*Trisopterus luscus*	1.00	1		1	1	1	1	1	1
Fish rays	*Raja clavata*	0.86	1				1	1	1	1
Fish rays	*Raja montagui*	0.14	1		1	1	1	1	1	1
Fish sea bream	*Spondyliosoma cantharus*	1.00				1	1	1	1	1
Fish seabass	*Dicentrarchus labrax*	1.00								
Fish sharks	*Mustelus mustelus*	0.37	1	1		1	1	1	1	1
Fish sharks	*Scyliorhinus canicula*	0.46	1	1	1		1		1	1
Fish sharks	*Scyliorhinus stellaris*	0.17	1		1	1	1		1	1
Fish sole	*Solea solea*	1.00	1			1	1		1	1
Fish sprat	*Sprattus sprattus*	1.00	1	1	1		1		1	1
Fish whiting	*Merlangius merlangus*	1.00	1		1	1	1		1	

Table S - 7 Fitted habitat species distribution models used to compute environmental driver maps for each trophic group of the eBoS Ecospace model. Models include: multiple regressions (Generalized Linear Model, Generalized Additive Model, Multiple Adaptive Regression Splines), regression trees (Boosted Regression Tree from GBM, Random Forest, Classification Tree Analysis), discriminant analysis (Flexible Discriminant Analysis) and learning techniques (Artificial Neural Network).

			habitat							
Ecopath trophic group	Latin name	Proportion in the group	MARS	ANN	CTA	FDA	GAM	GBM	GLM	RF
Benthic cephalopods	*Sepia officinalis*	1.00	1	1	1	1	1	1	1	1
Benthic inv. deposit feeders (Subsurface)	*Echinocardium cordatum*	0.66			1			1	1	1
Benthic inv. deposit feeders (Surface)	*Ophiothrix fragilis*	0.45	1	1	1	1	1	1	1	1
Benthic inv. deposit feeders (Surface)	*Pectinaria koreni*	0.15	1		1				1	1
Benthic inv. filter feeders	*Psammechinus miliaris*	0.15	1	1	1		1	1	1	1
Benthic inv. predators	*Asterias rubens*	0.03	1	1	1		1	1	1	
Benthic inv. predators	*Buccinum undatum*	0.11	1	1	1		1	1	1	1
Benthic inv. predators	*Owenia fusiformis*	0.66	1		1			1	1	1
Benthic inv. predators	*Sagartia troglodytes*	0.09								1
Benthopelagic cephalopods	*Alloteuthis subulata*	0.09								
Benthopelagic cephalopods	*Loligo vulgaris*	0.91								
Bivalvia inv. filter feeders	*Aequipecten opercularis*	0.02	1			1	1			
Bivalvia inv. filter feeders	*Ensis directus*	0.00			1	1		1	1	1
Bivalvia inv. filter feeders	*Glycymeris glycymeris*	0.61			1					
Bivalvia inv. filter feeders	*Lanice conchilega*	0.01	1		1	1		1	1	1
Fish Atlantic cod	*Gadus morhua*	1.00								
Fish dab	*Limanda limanda*	1.00	1	1	1	1	1	1	1	1
Fish benthos feeders	*Callionymus lyra*	0.48			1					

Fish benthos feeders	*Labrus bergylta*	0.07	1	1	1	1	1	1	1	
Fish benthos feeders	*Mullus surmuletus*	0.27								
Fish benthos feeders	*Zeus faber*	0.18								
Fish piscivorous	*Pollachius pollachius*	1.00								
Fish planktivorous	*Clupea harengus*	0.91								
Fish planktivorous	*Engraulis encrasicolus*	0.09								
Fish flounder	*Platichthys flesus*	1.00	1	1	1		1	1	1	1
Fish gurnard	*Chelidonichthys lastoviza*	0.30	1	1	1	1	1	1	1	1
Fish gurnard	*Chelidonichthys lucerna*	0.70			1					
Fish Atlantic horse mackerel	*Trachurus trachurus*	1.00								
King scallop	*Pecten maximus*	1.00	1	1	1	1	1	1	1	1
Fish mackerel	*Scomber scombrus*	1.00								
Fish pilchard	*Sardina pilchardus*	1.00								
Fish plaice	*Pleuronectes platessa*	1.00	1	1		1	1	1	1	1
Fish poor cod	*Trisopterus minutus*	1.00								
Fish pouting	*Trisopterus luscus*	1.00								
Fish rays	*Raja clavata*	0.86			1					
Fish rays	*Raja montagui*	0.14	1	1		1	1	1	1	1
Fish sea bream	*Spondyliosoma cantharus*	1.00								
Fish seabass	*Dicentrarchus labrax*	1.00			1					
Fish sharks	*Mustelus mustelus*	0.37	1	1	1		1	1	1	1
Fish sharks	*Scyliorhinus canicula*	0.46			1					
Fish sharks	*Scyliorhinus stellaris*	0.17	1	1	1		1	1	1	1
Fish sole	*Solea solea*	1.00								
Fish sprat	*Sprattus sprattus*	1.00								
Fish whiting	*Merlangius merlangus*	1.00								

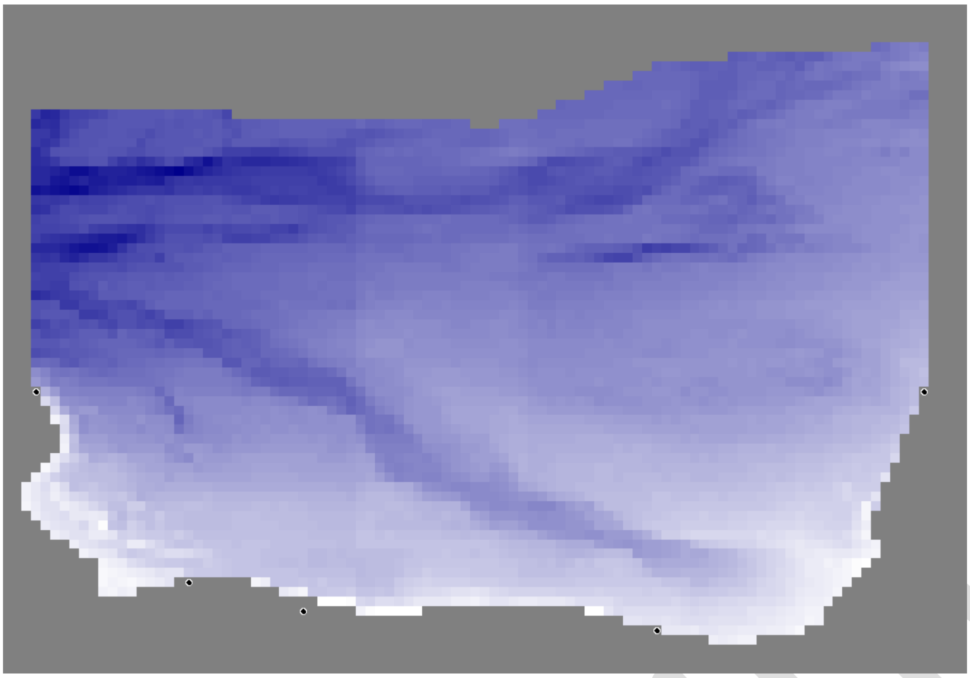

Figure S - 1 Base depth map from the General Bathymetric Chart of the Oceans.

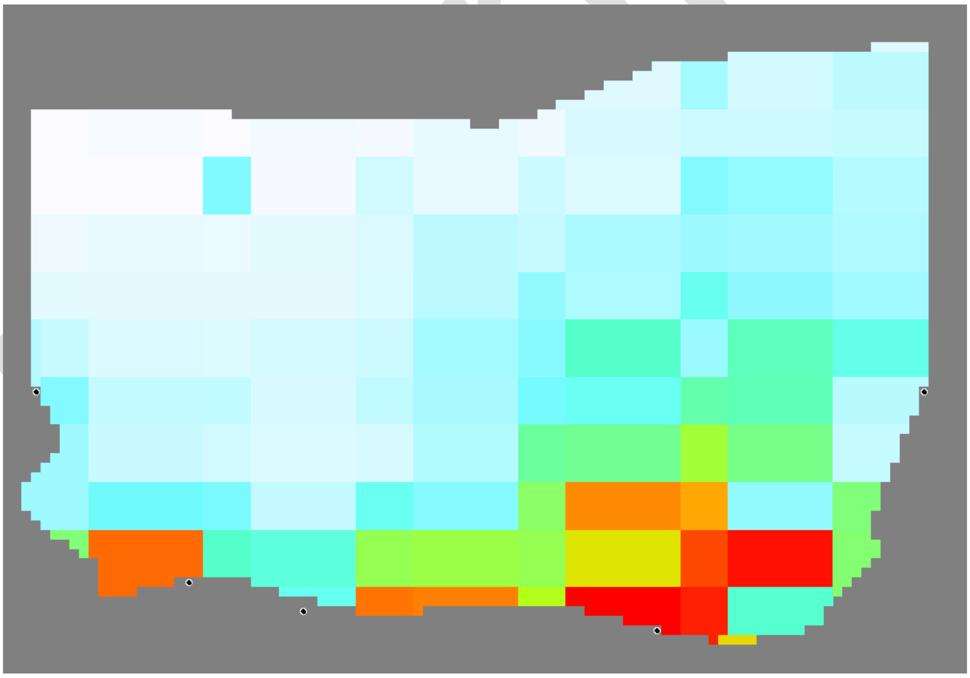

Figure S - 2 Primary production map from SeaWifs representing the relative chlorophyll a concentration in the bay in 2000

Table S - 8 Environmental driver used to model the reef effect for each trophic grous benefiting from it in the eBoS Ecospace model, derived from Raoux et al. (2017).

Area	**eBoS groups**	**Ecospace environmental driver inside the OWF**
Outside the OWF	All	0
Inside the OWF	Surface feeders sea birds	6.11
	Fish Atlantic cod	3.49
	Fish whiting	4.18
	Fish pouting	2.32
	Fish benthos feeders	2.07
	Fish sole	1.93
	Fish flounder	4.37
	Fish dab	4.37
	Benthic inv. predators	1.02
	Benthic inv. filter feeders	1.53
	Benthic inv. bivalves	2.2

Table S - 9 ES supply indicators description.

Ecosystem services	Description	Explanation
Provisioning service	Catch of commercial species by fishermen.	$\sum(C_{fish}) + \sum(C_{invertebrates})$ Where C are catches aggregated by group types.
Regulating service	Trophic pathways redundancy (Ulanowicz and Norden, 1990)	$\mathrm{R} = -\sum_{i,j=1}^{n} T_{ij}\log\left[\frac{T_{ij}^2}{T_i T_j'}\right]$ Where R 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. $RDC = \frac{\mathrm{R}}{DC}$ Where DC is the development capacity of the system.
Cultural service	Production of species of cultural importance	$\sum(P_{marine\ mammals}) + \sum(P_{sea\ birds})$

		Where P are production values of trophic groups. $P_{marine\ mammals} = P_{dolphins} + P_{seals} + P_{Harbour\ porpoises}$ $P_{sea\ birds} = P_{surface\ feeding\ birds} + P_{benthic\ feeding\ birds} + P_{plunge\ pursuit\ birds}$

Table S - 10 Changes in production of mid-trophic level groups due to the OWF

Groups	Delta production (%)
Benthic invertebartes predators	3,35
Fish limande	265,35
Fish flounder	345,79
Fish european plaice	-0,2
Fish sole	46,64
Fish sea bream	-6,25
Fish benthos feeders	67,22
Fish planctivorous	7,73
Fish piscivorous	-16,55
Fish european sprat	11,66
Fish european pilchard	12,24
Fish poor cod	12,65
Fish pouting	108,1
Fish gurnard	-6,93
Fish atlantic horse mackerel	9,8
Fish whiting	259,28
Fish atlantic cod	211,33
Fish sharks	0,41
Fish rays	1,57
Fish european seabass	2,59
Fish mackerel	0,81
Benthic cephalopods	-4,78
Benthopelagic cephalopods	-7,15

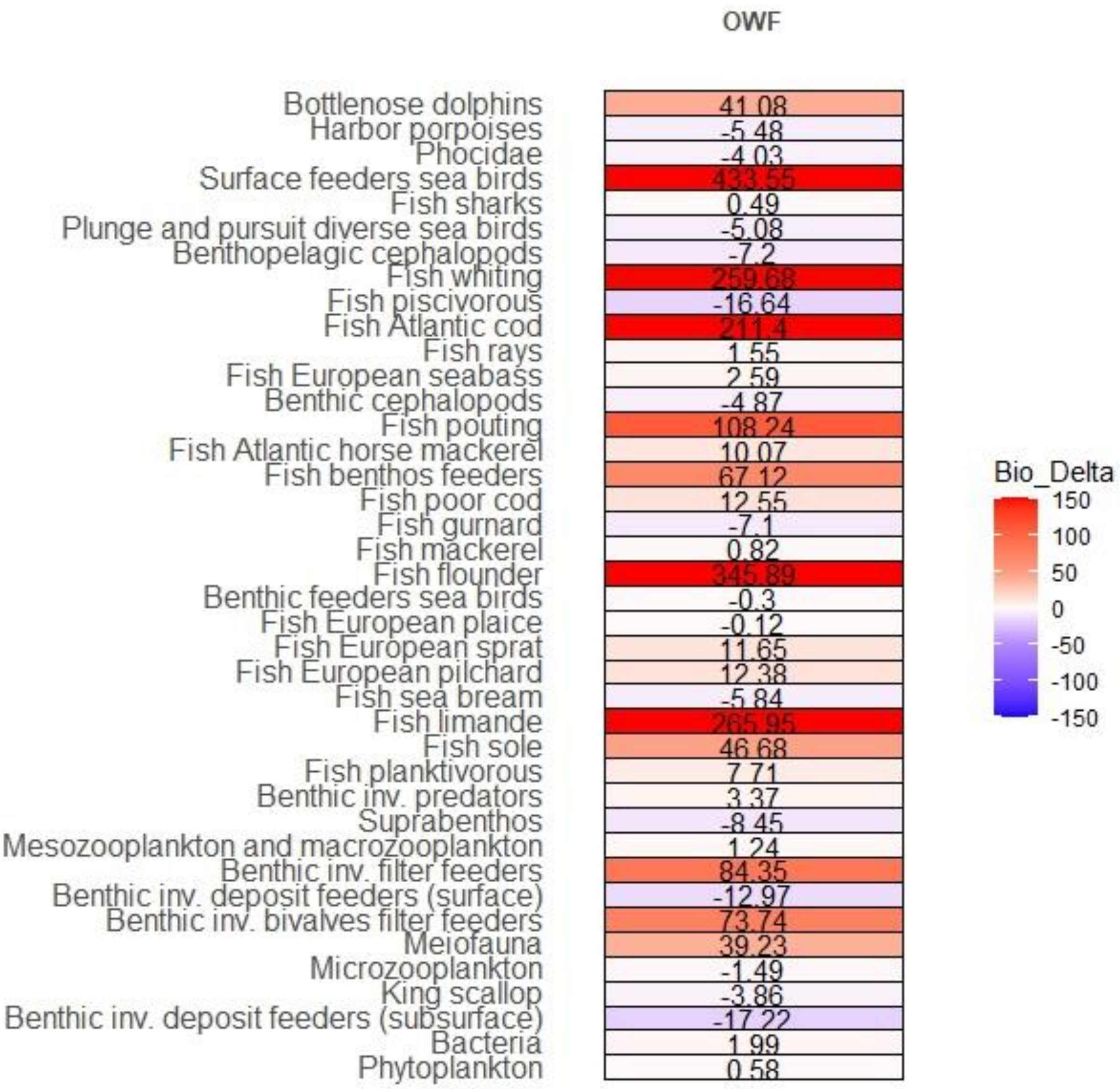

Figure S – 3 Effect of the OWF on trophic groups production inside the OWF (in percent compare to the reference model without the OWF).

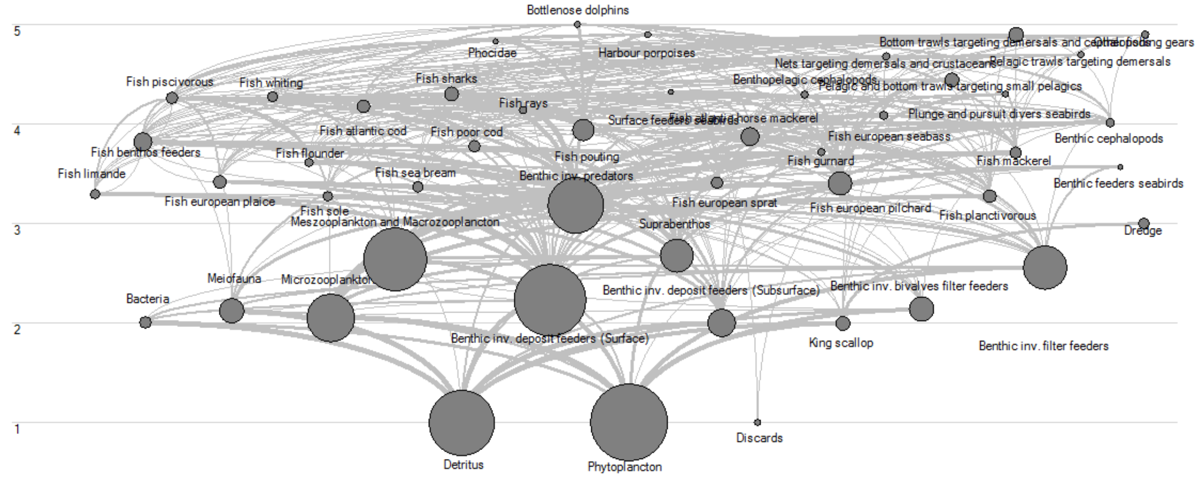

Figure S – 4 Food web model of the Bay of Seine developed by Halouani et al. (2020). Trophic groups are arranged using trophic level as y-axis. The size of each trophic group is proportional to the biomass it represents.