Cumulative effects of marine renewable energy and climate change on ecosystem properties: Sensitivity of ecological network analysis

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ARTICLE INFO

ABSTRACT

In an increasingly anthropogenic world, the scientific community and managers have to take interactions between the drivers of ecosystems into consideration. Tools like ecological network analysis (ENA) indices offer the opportunity to study those interactions at the ecosystem level. However, ENA indices have never been used to test the incidence of cumulative drivers. The present study uses models combining the effects of (i) the reef caused by the future offshore wind farm of Courseulles-sur-Mer and (ii) climate change on species distribution, to test the response of multiple ENA indices. ENA indices proved sensitive to this cumulative impact, displaying a wide variety of cumulative effects. They were also very powerful to characterize the role of the cumulative impact on ecosystem functioning. These results demonstrate the capacity of ENA indices to describe and understand cumulative effects at the ecosystem scale. Using a sensitivity analysis approach, this study shows that ENA indices could be viable tools for managers. To help them in their tasks, the next step could be to link ecosystem services to ENA indices for a more practical use.

1. Introduction

The world is in constant evolution, and human activities have deeply changed the rate of this evolution (Halpern et al., 2008b). Due to constant human activity, ecosystem functioning can no longer be dissociated from the dynamics of anthropogenic activities (Vitousek et al., 1997). Although coastal ecosystems are already heavily stressed, they are going to be increasingly exploited owing to the ever-increasing human population and demand for resources (Halpern et al., 2015). The English Channel – an epicontinental sea – is considered as one of the most anthropized marine ecosystems in the world (Halpern et al., 2008b; Dauvin, 2019). It is subjected to multiple anthropogenic drivers

such as marine transport, fishing, sediment dredging and aggregate extraction (Dauvin, 2019). It is also a hotspot for the future development of an offshore wind farm (OWF) in France (Pezy et al., 2020; Raoux et al., 2017). The effects of OWFs on ecosystems are divided in two phases: (i) the construction phase and (ii) the operational phase. The construction phase is characterized by short-lasting heavy disturbance (extreme noise from pile driving and vessels, cable-trenching disturbance), while the operational phase is associated to long-lasting effects on the environment (Hammar et al., 2014). One of the long-lasting effects of OWFs is the creation of new habitats and shelters for benthic and demersal species through the introduction of hard substrates in the surrounding soft substrate habitats (Wilhelmsson and Malm, 2008). The

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increased habitat heterogeneity can lead to changes in the abundance, biomass, and species richness of benthos and fish (Coates et al., 2014; Wilhelmsson et al., 2006), known as the reef effect. This reef effect is likely to be the main ecosystem effect of OWFs during the exploitation phase and can potentially affect the whole food web (Bergström et al., 2013). Only the exploitation phase is considered in this study, and the construction phase is ignored (De Mesel et al., 2015; Langhamer, 2012; Petersen and Malm, 2006).

To help managers and decision-makers in their sustainable development mission, it is a priority to understand how OWFs act on ecosystem dynamics, which is mainly driven by trophic interactions between species. Trophic network modeling can help to study those interactions. In a network, a stimulus on one part of the model can cascade throughout the network. Trophic network modeling is therefore an interesting tool to understand how drivers act on the whole ecosystem.

To analyze how food webs are affected by drivers, Ulanowicz (1997), Ulanowicz (2004) used ecological network analysis (ENA) indices. ENA indices can assess properties like the size, function or organization of a network through multiple metrics related to ecological processes, such as omnivory, recycling, overhead of flows (Borrett and Scharler, 2019; Heymans and Tomczak, 2016; Niquil et al., 2012a; Ulanowicz, 1986). These indices have been considered to be good potential indicators of the ecosystem health status and were thus cited by the OSPAR convention as promising indicators (Niquil et al., 2014; De la Vega et al., 2018; Safi et al., 2019). They were subsequently employed to understand the effects of human activities (e.g., the extension of a harbor) on ecosystems (Tecchio et al., 2016), or even to develop different management scenarios (Heymans and Tomczak, 2016; Tomczak et al., 2013).

Raoux et al. (2017) explored a new way to look at the potential effects of OWFs through food web models and flow analysis. These authors implemented the Ecopath with Ecosim (EwE) approach (Christensen and Walters, 2004; Heymans et al., 2011; Polovina, 1984) to model the food web at a planned OWF (Courseulles-sur-mer, Bay of Seine, English Channel, France). One of their main results was that the total ecosystem activity, recycling, and the ecosystem maturity increased after OWF construction, due to the reef effect (Raoux et al., 2017, 2019). Results also indicated an anticipated increase in detritivory flows and an increased benthic fish biomass after OWF construction.

However, one of the main weaknesses of impact studies is that they focus on a single ecosystemic driver (Raoux et al., 2018), and ignore the other drivers of disturbance with long-lasting effects such as climate change (Hoegh-Guldberg and Bruno, 2010). The main issue when ignoring combined drivers is to miss cumulative effects that may alter the magnitude or direction of predicted changes (Breitburg et al., 1998; Vinebrooke et al., 2004; Fu et al., 2018; Planque et al., 2010). Hence, irrelevant or misleading recommendations can be issued when cumulative effects are not included (Halpern et al., 2008a).

We propose to investigate the cumulative effects of climate change and one OWF using ecological network analysis on a food web model. To do so, we transformed the Raoux et al. (2017) Ecopath model of the future Courseulles-sur-Mer OWF into a Linear inverse model (LIM). We coupled this OWF LIM model with niche models of the Courseulles-sur-Mer ecosystem (Ben Rais Ben Rais Lasram et al., 2020) to study the effects of climate change on species. Several representative concentration pathway (IPCC 2014) scenarios were used to simulate changes in the bioclimatic niches of 72 macrofauna species with dominant biomass within the trophic compartments of the food web.

We used those scenarios combining the effects of climate change and the OWF to compute a series of ENA indices to study the effects of each driver separately and then of the combined drivers on the food web of Courseulles-sur-Mer. We explored the capacities of ENA indices to study cumulative effects. Finally, we discussed the advantages and weaknesses of a framework based on ENA indices to investigate cumulative impacts and provide management recommendations.

2. Materials and methods

2.1. Study area

This study is focused on the area of the future OWF of Courseulles-sur-Mer (Normandy, France), that will be located in the lower middle part of the Bay of Seine (Fig. 1). The bay opens onto the English Channel in its northern part, its depth is relatively shallow with a mean of 30 m at the future OWF location. The OWF area will cover 50 km², and 64 offshore wind turbines are planned. The OWF will be built on coarse sand and sandy gravels harboring benthic communities of the Bay of Seine (Baffreau et al., 2017).

2.2. Cumulative impact models

In order to test ENA indices in cumulative impact scenarios, we created trophic models based on two studies: (i) a trophic modeling of the expected reef effect caused by the future Courseulles-sur-Mer OWF (Raoux et al., 2017), and (ii) results from niche models simulating climate change (Ben Rais Ben Rais Lasram et al., 2020).

2.2.1. Wind farm effect on the food web

The construction of turbines and their associated scour protection creates new hard-substrate habitats and shelters such as artificial reefs. These new hard-substrate habitats increase habitat heterogeneity, leading to increased abundance, biomass, and species richness of the benthic macrofauna (e.g., the mussel (*Mytilus edulis*)) and of demersal fish (e.g., the pouting (*Trisopterus luscus*)) (Coates et al., 2014; Raoux et al., 2017; Wilhelmsson et al., 2006).

The reef effect of the future Courseulles-sur-Mer OWF was modeled using trophic network models quantifying the flows of energy between organisms, as described in Raoux et al. (2017). This trophic model was based on the Ecopath with Ecosim approach (Christensen and Walters, 2004; Polovina, 1984). A first Ecopath model was built to model the ecosystem before the establishment of the OWF. Ecopath is a mass balance model, meaning that the sums of the inflows and outflows of the system are equal. It was used as a basis for an Ecosim model. Ecosim is a time dynamic model based on the mass balance Ecopath model (Pauly et al., 2000). It was used to model the reef effect of the future Courseulles-sur-Mer OWF and to create an Ecopath model 30 years from the OWF construction. Two Ecopath models were thus created: a baseline Ecopath model called BOWF (before offshore wind farm), and a model called REEF, based on the reef effect demonstrated to be the main long-term effect of the farm (Raoux et al., 2017). Both models were composed of the same 37 compartments of species, with similar trophic interactions (Leguerrier et al., 2003).

While the Ecopath approach is a well acknowledged mass balance approach, it can be criticized for its limitations in the modeling of low-trophic-level compartments – which are often subjected to high inter and intra year biomass variability – and because the method is based on a manual balancing procedure, which is not based on uncertainty evaluation of the input parameters. In order to take into account the uncertainty in the input parameters but also to define uncertainty in the outputs (flow values or ENA indices), another mass balance modeling approach is more suitable, i.e., the LIM linear inverse models, Monte Carlo Markov Chain or LIM-MCMC (Niquil et al., 2012b; Van Den Meersche et al., 2009). Linear inverse modeling relies on a set of linear equalities and inequalities to estimate unknown flows in food webs. The equalities set the mass balance of the model, while the inequalities correspond to the confidence intervals of the measured flows. The Monte Carlo method is a sampling procedure used to determine the complete coverage of the range of possible solutions. Which means that while Ecopath only considers one value for each parameter/flow, LIM-MCMC integrates a range of values to represent the variability of living organisms (Meersche et al., 2009; Niquil et al., 2012b; van Oevelen et al., 2010). This variability is also very useful to compare models
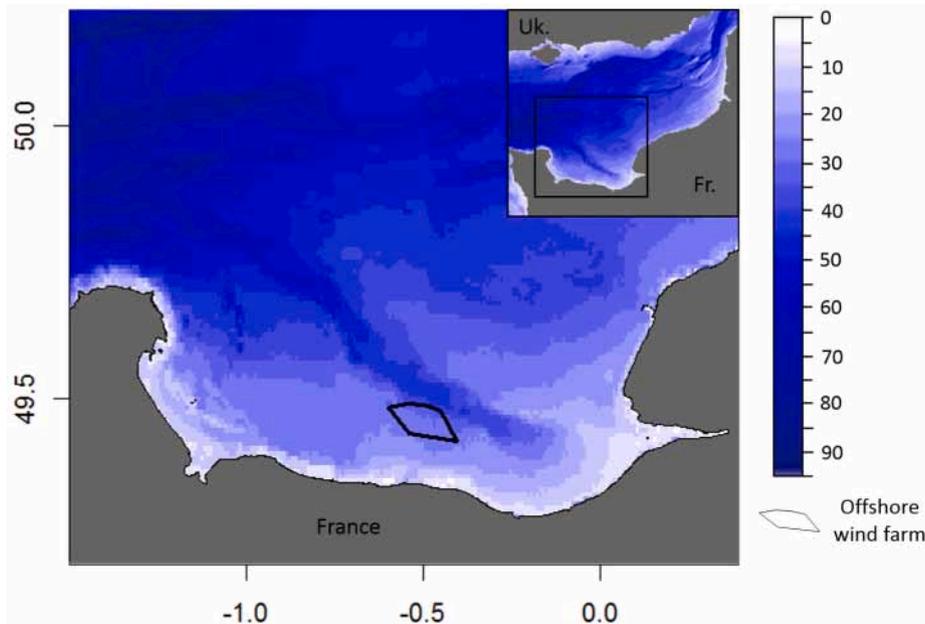
Fig. 1. Localization of the future offshore wind farm of Courseulles-sur-Mer in the Bay of Seine.

statistically.

We thus used the BOWF and REEF Ecopath models of Raoux et al. (2017) and transformed them into linear inverse models (LIMs). Four steps are necessary to create a LIM model, in which we determined:

- The topology of the network based on the possible flows
- The mass balance equations
- The constraints of the model
- The computing parameters (jump and iterations).

Because the two Ecopath models used the same topology, we based our topology on them. However, we had to reduce the number of biological compartments to shorten the computation time. The number of compartments decreased from 37 to 19 (Fig. 2, Table A.1), and aggregation was based on the diet of each Ecopath compartment (Tables A.1, A.3 & A.4; Leguerrier et al., 2003). Keeping the same topology between the LIM BOWF model and the LIM REEF model allowed us to compare the results of the two models free of any structural bias (Tables A.3 & A.4).

We defined the mass balance equation for each compartment. In a mass balance equation, the input of a compartment is equal to its output. The input is the consumption of the compartment, while the output is the excretion, the respiration and the production of the compartment available for the system (predation).

Production (P) = consumption (Q) – excretion (U) – respiration (R)

Regarding the constraints of the model, we set minimum and maximum values for parameters such as the production to biomass ratio (P/B), the production to consumption ratio (P/Q), the respiration to consumption ratio (R/Q), and the excretion to consumption ratio (U/Q) (Table A.2). We used constraint values from the literature for some compartments, while others were computed with the Ecopath values and pedigrees. Pedigrees were used to define the uncertainty around the Ecopath values to determine minimum and maximum values (Table A.2). When the Ecopath values were considered very reliable ('Fish, planktivorous', 'Fish, benthos feeders', 'Fish, piscivorous' and 'Flat fish'), the uncertainty around the P/B, P/Q and U/Q values was set
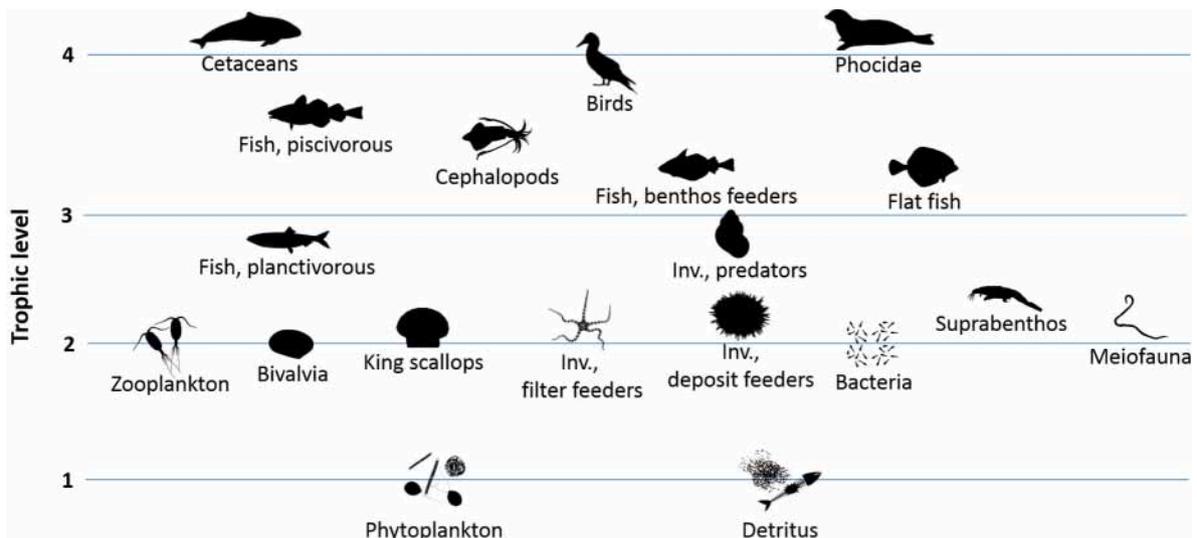

Fig. 2. Functional compartments of the Courseulles-sur-Mer ecosystem model organized according to their trophic level, based on the BOWF trophic levels.

to 10%. The diet constraints were calculated with the same method for all compartments of the models (BOWF and REEF). Finally, we added primary production values to drive the two LIM models: while the Ecopath model does not consider primary production values, the LIM model needs minimum and maximum values of potential primary production (Behrenfeld and Falkowski, 1997; Napoléon and Claquin, 2012).

The xsample function from the LIM package was used to compute the LIM models (Meersche et al., 2009). The LIM-MCMC model depends on two parameters for its computing: the jump and the number of iterations. With the equations and the constraints, the LIM MCMC model creates a polytope of solution that includes all the possible values for each flow of the system. The number of iterations indicates the number of solutions sampled in the space of solution. The mean distance between iterations is the jump. If the sampling goes outside the space of solution, it will bounce back (mirror technique) inside the space. A jump of 0.05 gC.m^{-2} and 500,000 iterations was chosen after testing the mean shifting value/variability of the biggest flows in order to properly sample solutions.

2.2.2. Climate change simulation

In order to assess cumulative impacts through a trophic modeling approach, we had to integrate the climate change effect in both LIM trophic models. To evaluate the effect of climate change, we used results from the niche models published in Ben Rais Ben Rais Lasram et al. (2020). Niche model algorithms are correlative approaches aimed at identifying the potential species niches by correlating species occurrences to environmental variables such as temperature, salinity or other parameters. Niche models were built with an ensemble modeling procedure combining different modeling techniques. Future climate change projections for 72 species of the Bay of Seine were based on the "business as usual" representative concentration pathway scenarios (Intergovernmental Panel on Climate Change, RCP 8.5) at the 2091–2100 time steps (Ben Rais Lasram et al., 2020).

The compartments of the LIM trophic model were not all simulated in the niche model approach. Consequently, we focused on integrating the niche model results of the commercially exploited compartments, which included 4 fish compartments – Fish, benthos feeders (FBF); Flat Fish (FFI); Fish, Piscivorous (FPI); Fish, Planktivorous (FPL) – and 2 mollusk compartments – Cephalopods (CEP); King Scallop (KSC). Those compartments represented the compartments impacted by climate change.

To integrate the results of the niche models into the trophic models, we linked the evolution of the suitability index of the niche models to biomass according to Chaalali et al. (2016). We used the evolution of the suitability index C to multiply the biomass of the species by (1-C) to reflect the biomass changes:

$$C = \frac{P_{ref} - P_{rcp}}{P_{ref}}$$

where P_{ref} is the suitability index of the species in the current niche model and P_{rcp} the suitability index of the species in RCP 8.5.

As the production to biomass ratio (P/B) of fish is based on temperature (Lassalle et al., 2011), the P/B ratios of all the fish compartments impacted by climate change were modified following the temperature values of the RCP 8.5 scenarios (Table A.6). We used the

temperature values corresponding to the habitats of each compartment (surface temperature for the pelagic compartments, sub-surface temperature for the bentho-pelagic compartments, and bottom temperature for the benthic and demersal compartments). In a mass balanced condition, the P/B ratio of fish species is considered to be equal to the instantaneous coefficient of total mortality (Z) (Fig. 3):

$$Z = M + F$$

where M is natural mortality and F is fishing mortality, and M is calculated from the empirical equation:

$$M = K^{0.65} \times L_\infty^{-0.279} \times T^{0.463}$$

where K is the curvature parameter of the von Bertalanffy growth function (VBGF), while L∞ is the asymptotic length and T the mean environmental temperature in °C depending of the depth.

We computed new P/B ratios by changing the temperature in the natural mortality equation (M) without changing fishing mortality (F) so as to be coherent. The evolution of natural mortality was then applied to the P/B ratio of each fish compartment. If natural mortality increased by 10% for a fish species owing to the new temperature, we increased the P/B ratio of the species by 10% in the climate change scenario.

We had to use different methods for the Mollusk compartments. There was no equation connecting the P/B ratio with temperature for cephalopods. We therefore used the cephalopod feeding rate equation because of its link to temperature (O'Dor and Wells, 1987):

$$Feeding\,rate = 0.058 \times W^{0.79} \times 1.082^T$$

where W is the body mass in g and T is temperature in degrees Celsius.

We computed a new feeding rate for cephalopods with the niche model. The evolution of the feeding rate between the current and the future RCP 8.5 temperatures allowed us to estimate the P/B ratio of the cephalopod compartment. We used a food conversion rate of 30% for cephalopods (Boyle and Rodhouse, 2005).

For king scallops, we used the growth rate equation (Laing, 1999). The equation was verified by comparing the temperature estimated from the RCP 8.5 scenarios with the temperature ranges applied in growth experiments (Chauvaud et al., 2012; Laing, 2000). The temperature estimated with the RCP model was sustainable by *Pecten maximus in situ* and *ex situ* (15.3 °C), and resulted in increased production:

$$Growth\,rate = 0.0199 \times T - 0.081$$

We thus changed the P/B ratio of the king scallop compartment according to the evolution of its growth rate between the current temperature and the future temperature under the RCP 8.5 scenario.

2.2.3. Ecological network analysis

With their 19 compartments each, the LIM models contained a flow matrix of 144 flows. We computed multiple metrics to analyze the ecological properties of each model. We first computed the through-flow/activity of (i) each compartment (sum of all the inflows/outflows) (Table A.1), (ii) the import (IMP), and (iii) respiration (RES) to understand the effects of the climate change and of the OWF at the flow matrix level. We also computed ENA indices (Table 1). ENA indices summarize
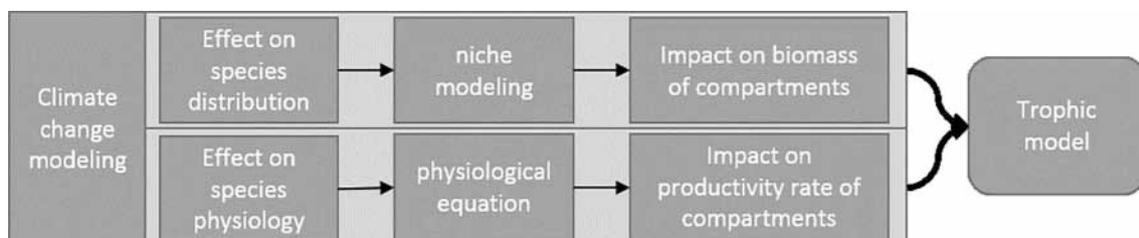

Fig. 3. Schematic representation of the climate change modeling approach.

Table 1
ENA indices computed with the LIM models results.

Name	Objective	Calculation	References
Total activity of the system or Total System Throughput (T..)	The total system throughput is equal to the sum of all the flows in the system. It is a network level indicator of the size and activity of the system.	$T_{..} = \sum_{i,j=1}^{n} T_{ij}$ where T_{ij} is the flow between compartments j and i.	Finn (1976), Ulanowicz and Norden (1990)
Average Mutual Information (AMI)	Average mutual information measures the organization of a network, the more web-like the system is, the lower the AMI should be.	$AMI = k \sum_{i=1}^{n+2} \sum_{j=0}^{n} \frac{T_{ij}}{T_{..}} log_2 \frac{T_{ij}T_{..}}{T_{i.}T_{.j}}$	Gallager (1968), Latham (2006)
Ascendency (A)	Ascendency is a measurement of the growth of the system, integrating its size (T..) and its organization (AMI)	$A = \sum_{i=1}^{n+2} \sum_{j=0}^{n} T_{ij} log_2 \frac{T_{ij}T_{..}}{T_{i.}T_{.j}}$ $A = AMI \times T_{..}$	Ulanowicz (1980), Ulanowicz (1986), Latham (2006)
Development capacity (DC)	The total development capacity is the upper limit of ascendency, it represents the maximum development of the system.	$DC = \sum_{i=1}^{n+2} \sum_{j=0}^{n} T_{ij} log_2 \frac{T_{ij}}{T_{..}}$	Latham (2006)
Overhead (R)	The overhead is the "reserve" of the system information and refers to the extent of parallel flows in the system	$R = DC - A$	Ulanowicz et al. (2009), Ulanowicz and Norden (1990)
Detritivory to herbivory ratio (D/H)	The detritivory to herbivory ratio is the ratio of detritus consumption (Detritivory) compared to the consumption of primary producers (Herbivory) in the ecosystem.	$D/H = \frac{(\sum DET)}{(\sum PP)}$ where DET is the flow of detritus consumption and PP the flow of consumption by primary producers	Latham (2006)
System omnivory (SOI)	The system omnivory index quantifies the distribution of trophic interactions among different trophic levels.	$OI_i = \sum_{j=1}^{n} \left[TL_j - (TL_i - 1) \right]^2 \times DC_{ij}$ $SOI = \frac{\sum_{i=1}^{n} [OI_i \times log(Q_i)]}{\sum_{i=1}^{n} log(Q_i)}$ 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.	Odum (1985)
Mean Trophic Level (MTL)	The mean trophic level is the mean trophic level of the network's compartments. It is based on the compartments' trophic levels. Its values can be 1 (primary producers and detritus), 2 (all consumers), and can reach > 4 (top predators).	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ where B is the biomass of i or j.	Latham (2006)

the emergent properties of the ecosystem. A range of indices was chosen according to previous recommendations about their use by ecosystem managers (Fath et al., 2019; Safi et al., 2019).

2.2.4. The different types of cumulative effects

Sixteen models were computed to test ENA indices in multiple scenarios. The models included:

- The reference BOWF model
- The REEF model
- The climate-change-only scenarios, based on the LIM BOWF model, with each of the selected compartments impacted by the climate change effect and an extra model (BOWFTOT) combining all the compartments impacted at once
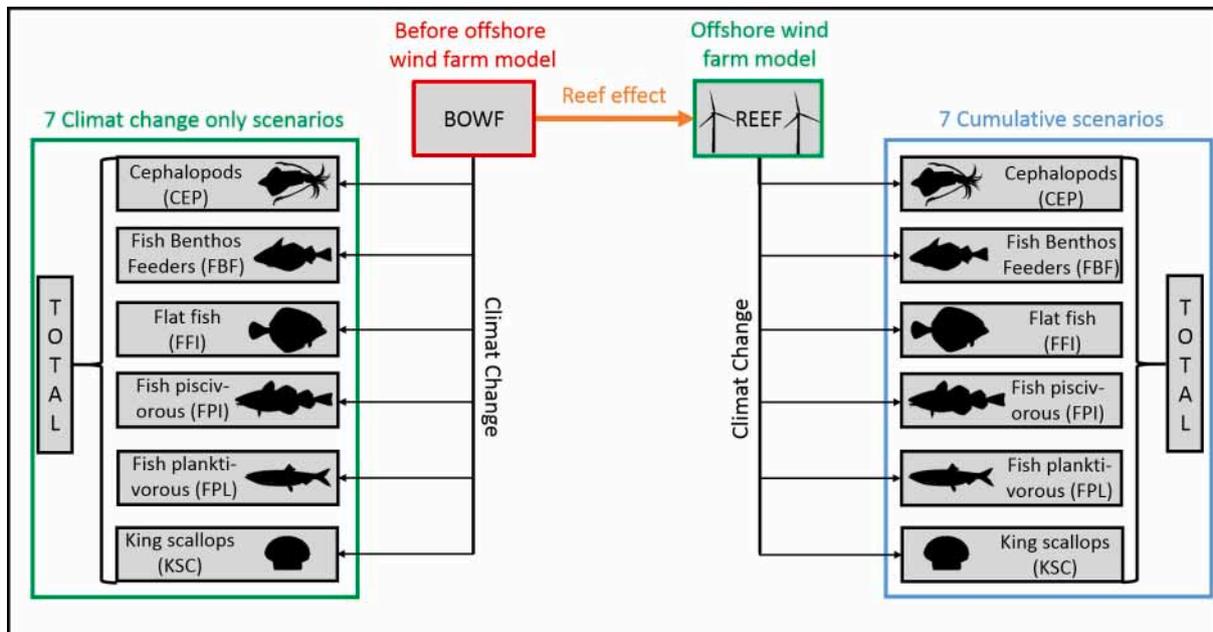
Fig. 4. Modeling framework of the sixteen models all represented by gray boxes, with the initial BOWF model, single effect models including seven climate change scenarios and the REEF model, and the combined models including seven cumulative scenarios.

- The cumulative impact scenarios, based on the LIM REEF model, with each of the selected compartments impacted by the climate change effect and an extra model (REEFTOT) combining all the compartments impacted at once.

Each model was named according to its initial model (BOWF or REEF) and to the name of the impacted compartment if impacted by climate change (Fig. 4).

We followed this framework (Fig. 4) to analyze the combined effects of climate change and of the reef effect depending on the impacted compartment. We used the same methodology as Fu et al. (2018) to characterize the combined effect on each ENA index and for each scenario.

First, we computed the relative index variation between the reference BOWF model and a single effect model (reef effect only or climate change only) for each ENA:

$$\Delta I_k^{sep} = \frac{I_k - I_c}{I_c}$$

where I_c is the index value of the reference model and I_k the index value of a single-effect model (reef only or CC only).

Then, we summed the variation (ΔI_k^{sep}) of each single effect in a same scenario to get the reef + climate change additive effect:

$$\sum \Delta I_k^{sep}$$

We also computed the cumulative effect as the variation between the initial BOWF model and the cumulative impact scenario (reef effect and climate change effect) for each ENA (ΔI_k^{cum}):

$$\Delta I_k^{cum} = \frac{I_k - I_c}{I_c}$$

To determine the combined effect, we compared the additive effect variation with the cumulative effect variation. If the two variations were equal, the effect was considered additive:

$$\Delta I_k^{cum} = \sum \Delta I_k^{sep}$$

If the additive effect variation was lower than the cumulative effect variation and both variations were positive or negative, the response was synergistic positive or negative:

Synergistic positive: $\Delta I_k^{cum} > \sum \Delta I_k^{sep} > 0$
Synergistic negative: $\Delta I_k^{cum} < \sum \Delta I_k^{sep} < 0$
If the additive effect variation was higher than the cumulative effect

variation while both variations were positive or negative, the response was dampened positive or negative.

If the additive effect variation was opposite to the cumulative effect variation, the response was antagonistic. When the combined effect variation was positive, it was a positive antagonism, and *vice versa* for negative antagonism (Fig. 5).

2.2.5. Statistical comparison

Indices were calculated for each solution of the LIM models (500,000 solutions quantifying each flow for each model). A previous study showed that parametric tests like Student's T-tests could identify differences even for tiny effects (Tecchio et al., 2016). The non-parametric Cliff delta (Cliff, 1993) was chosen for its better suitability (Valérie Girardin & Justine Lequesne, pers. com., Laboratoire de Mathématiques Nicolas Oresme, Tecchio et al., 2016). The same threshold as Romano et al. (2006) and MacBeth et al. (2012) was used considering the differences between the datasets: negligible if the Cliff delta ($| \partial \text{Cliff} |$) was < 0.147, low if < 0.33, medium if < 0.474, or strong if > 0.474.

The Cliff delta was used to compare single effect models ("reef only" and "climate change only" scenarios) to the initial reference BOWF model and to compare the REEF model with the cumulative impact scenarios (reef effect + climate change effect). This was applied to the throughflow/activity (input/output) of each compartment as well as on the ENA. The delta also allowed us to compare the additive effect variation (ΔI_k^{sep}) with the cumulative effect variation (ΔI_k^{cum}). If the difference was considered medium ($| \partial \text{Cliff} | < 0.33$), the cumulative effect was considered different than the additive effect. We determined the cumulative effect depending on the difference between the additive effect variation and the cumulative effect variation (Fig. 5).

To reduce the number of models when describing the ENA indices, we used an average unweighted pair group method with arithmetic mean (UPGMA) based on Euclidean distance. The UPGMA compared all the different models according to their mean ENA values.

3. Results

3.1. Reef effect on the food web

When the reef effect of the offshore wind farm was modeled in the LIM model, it resulted in an increased activity of the benthic compartment and in a decreased activity of the pelagic compartment. The reef effect also resulted in increased detritus consumption, increased phytoplankton activity and increased import (Fig. 6).
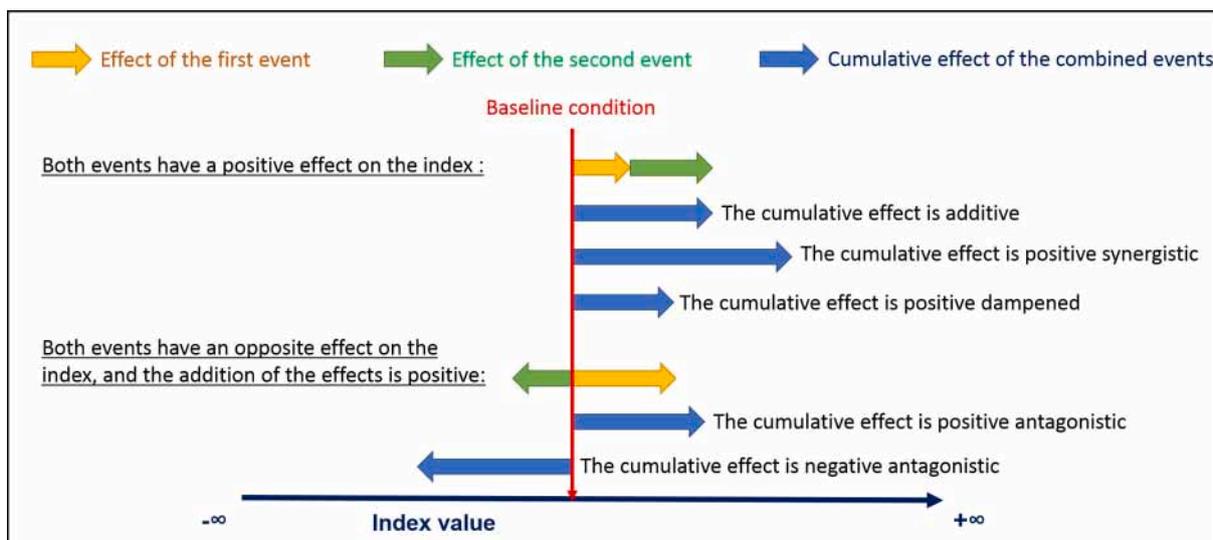

Fig. 5. Different types of cumulative effects on the different index values (e.g., ENA index).
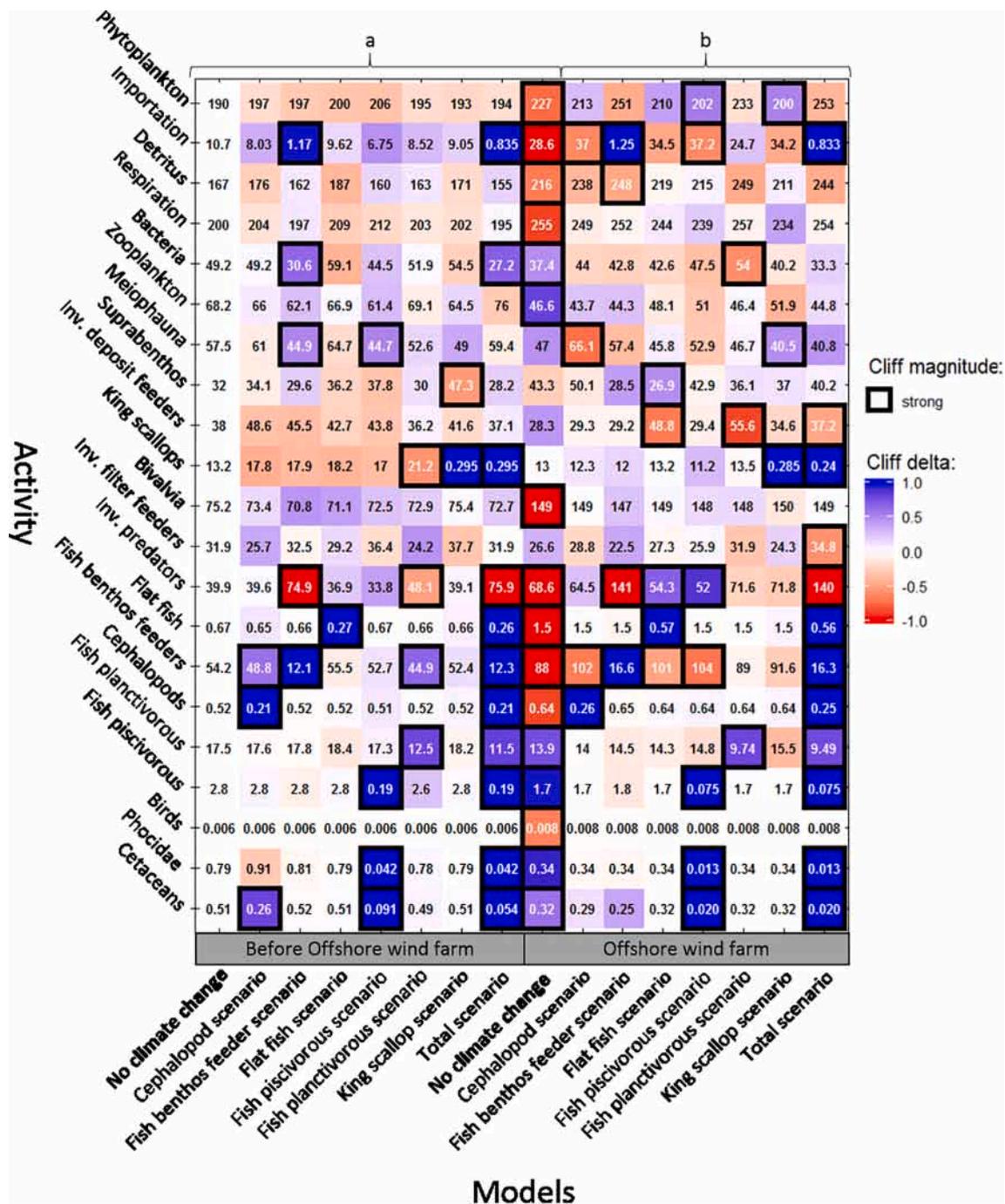
Fig. 6. Variation of all the throughflow/activity (input/output) in gC.m^2 between: the BOWF model and the single effect models (reef effect or climate change effect, a group on the left), and between the REEF model and the cumulative models (reef effect + climate change effect, b group on the right). Red, increased activity; blue, decreased activity; bold-bordered square, strong variation according to the cliff delta ($| \partial$Cliff $| < 0.474$).

3.2. Effects of climate change on the food webs before offshore wind farm construction

When the BOWF models were impacted by the climate change scenarios, three compartments displayed a strong increase in activity and 11 displayed a strong decrease in activity. Throughout the compartments and scenarios, climate change had mainly a negative effect on compartment activity. Negative effects on activity can be divided into two types: (i) the direct effect of climate change on the targeted compartment (for instance, lower biomass of the cephalopod compartment in the cephalopod scenario leading to lower cephalopod activity), and (ii) the indirect / cascading effect of climate change on activity

(lower biomass of the cephalopod compartment in the cephalopod scenario leading to lower cetaceous activity) (Fig. 6).

3.3. Combined effects of climate change and of an offshore wind farm on the food web

When the offshore wind farm (REEF) models were impacted by the climate change scenarios, 8 compartments showed a strong increase in activity and 13 a strong decrease in activity. The REEF scenarios displayed greater changes due to climate change than the BOWF scenarios (38 strong variations in total for the REEF scenarios *versus* 30 for the BOWF scenarios), with a relatively more positive effect on activity.

Similarly to the BOWF scenarios, the negative effects on activity were of two types: (i) the direct effects, and (ii) the indirect / cascading effects. While the direct effects of climate change appeared to be similar in the BOWF and REEF scenarios, the indirect / cascading effects were mostly different. There were four similarities between the BOWF and REEF models among the twenty indirect effects of climate change: (i) the indirect increase in invertebrate predator activity in the total scenario and the "fish, benthos feeders" scenario, (ii) the indirect decrease in phocidae activity in the total scenario and in the "fish, piscivorous" scenario, (iii) the indirect decrease in cetaceous activity in the total scenario and in the "fish, piscivorous" scenario, and (iv) the indirect decrease in import in the total scenario and the "fish, benthos feeders" scenario (Fig. 6).

3.4. Changes in the structure and functioning of the food web

The flow matrices were used to compute the ENA indices. The UPGMA discriminated five groups of models. The models including the sole climate change effect and the BOWF model formed three groups (with two groups composed of only one model). The models including the reef + climate change effect formed two groups (Fig. 7, A).

In both the BOWF and REEF scenarios, the "fish, benthos feeders" (FBF) scenario and the total (TOT) scenario showed differences with the rest of the climate change scenarios (Fig. 7, B). Those models showed a greater number of strong differences ($|\partial Cliff| > 0,474$) with their respective reference model compared to the other scenarios. Four strong differences were observed under the BOWFTOT model compared to BOWF, six under BOWFFBF compared to BOWF, and three under REEFTOT and REEFFBF compared to REEF.

The climate change effects on the "fish, benthos feeders" (FBF) scenario and the total (TOT) scenario appeared as structuring as the REEF effect itself (Fig. 7, A & B). The climate change effect strongly impacted

($|\partial Cliff| > 0.474$) four indices of the total scenario and six of the "fish, benthos feeders" scenario, while the reef effect strongly impacted six indices. The remaining climate change scenarios had little effect on the system (Fig. 7, B).

3.5. Cumulative effects on ENA indices

The cumulative impact assessment showed a wide variety of cumulative effects – additional, synergetic, dampened, and antagonistic. Six of the seven scenarios showed at least one cumulative effect on their ENA ($0.33 < |\partial Cliff|$). As for ENA indices, seven out of eight indices in total showed at least one cumulative effect ($\Delta Iksep \neq \Delta Ikcum$) (Fig. 8).

Most of the cumulative effects were additive ($\Delta Iksep = \Delta Ikcum$) for all the results (all ENA indices for all models). Sixteen percent of the models showed a cumulative effect ($\Delta Iksep$ different from $\Delta Ikcum$ with $|\partial Cliff| > 0.33$).

4. Discussion

This study assesses the cumulative impacts of climate change and an OWF on the Bay of the Seine food web, based on LIM models. Because of the complexity of modeling climate change in its full extent (Larocque et al., 2011), this work was focused on the effect of climate change on the indigenous species of the bay, more particularly on commercially exploited species. That is why it is a sensitivity analysis of these cumulative impacts on ENA indices. First, our sensitivity analysis revealed that each effect taken separately had an impact on the functioning and organization of the ecosystem. The "fish, benthos feeders" compartment appeared particularly sensitive to the two single effects. When the effects were combined, we observed significant cumulative effects on multiple ENA indices for multiple scenarios. Those significant cumulative effects led to unexpected effects on the ecosystem. Overall, ENA
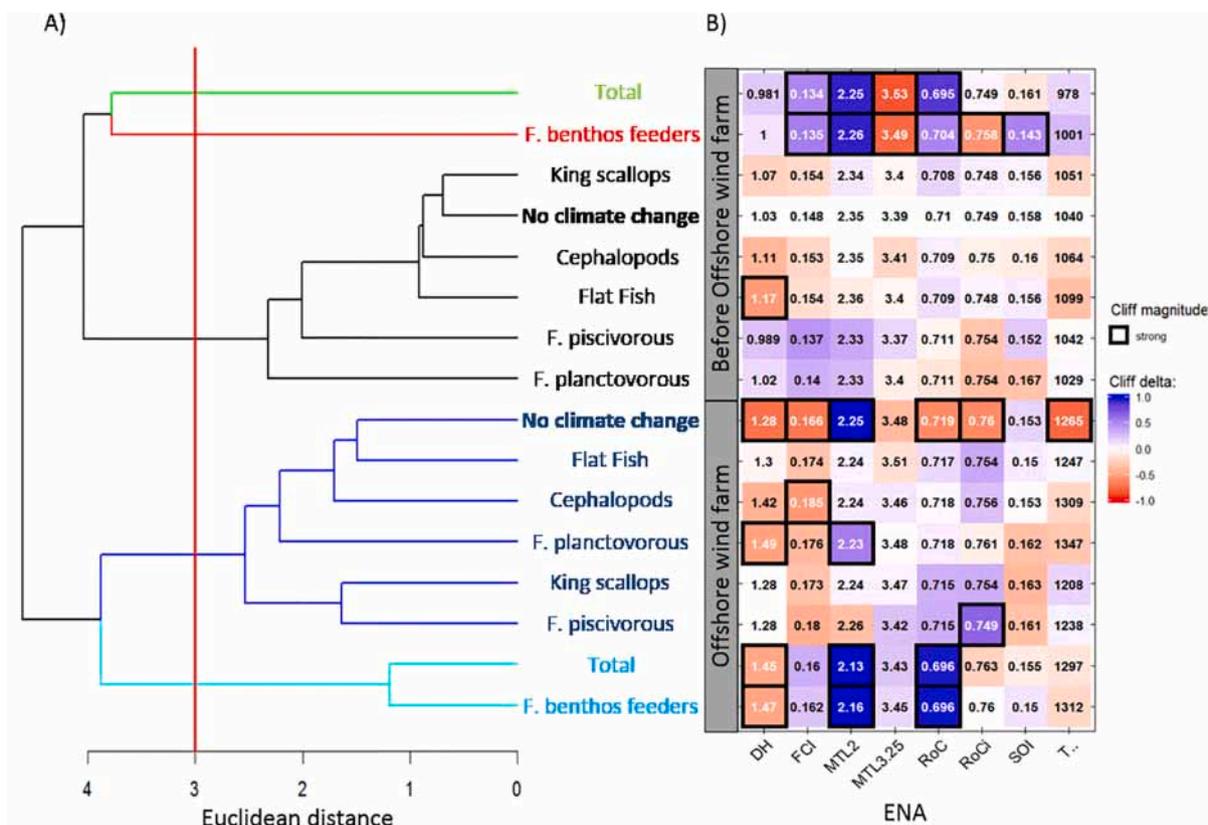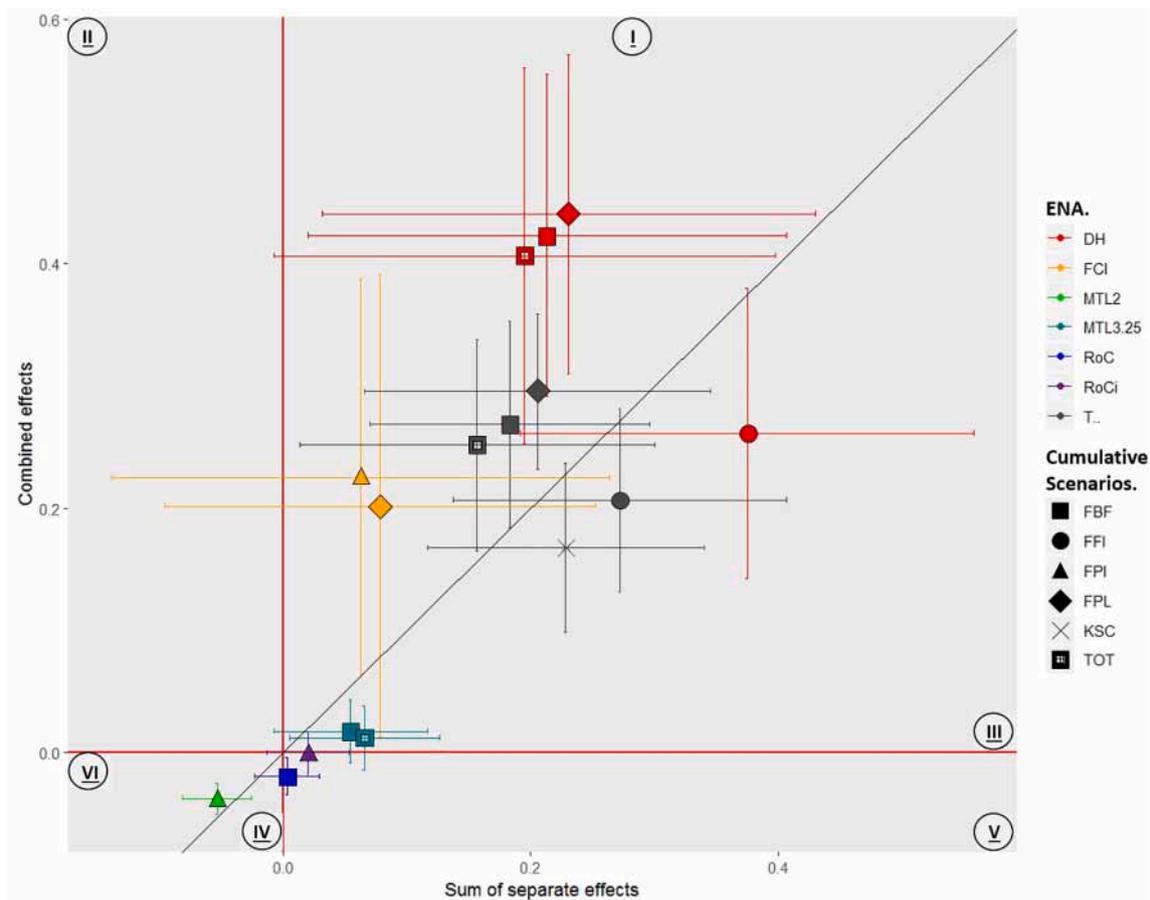

Fig. 7. A) Following UPGMA to determine different groups of models, 5 groups were selected. B) The Cliff delta was used to compare the ENA results of: the BOWF model and the single effect models (reef effect or climate change effect), and between the REEF model and the cumulative models (reef effect + climate change effect).

Fig. 8. Cumulative effects of the different scenarios on multiple ENA indices. Each cumulative effect is represented in a zone. Zone I, positive synergistic effect; zone II, positive antagonistic effect; zone III, positive dampened effect; zone IV, negative synergistic effect; zone V, negative antagonistic effect; and zone VI, negative dampened effect.

indices appeared sensitive to the cumulative impact.

4.1. The structuring role of the reef effect

The results of the REEF model seem to suggest a regime shifting towards a new stable state. An ecosystem shift is documented as a change at several trophic levels leading to ecosystem restructuring (Andersen et al., 2009; Lees et al., 2006). The restructuring of the system should be visible on the ecosystem structure but also on its functioning. The restructuring due to the reef effect was already predicted by Raoux et al. (2017), Raoux et al. (2019) based on the evolution of the mean trophic level (MTL 2). We modeled a similar decrease in MTL 2 between the BOWF and REEF models. A decline in MTL 2 would explain a transition in the food web from long-lived high-trophic-level organisms like piscivorous fish towards short-lived low-trophic-level organisms such as invertebrates and planktivorous fish (Pauly et al., 1998). In the reef effect case, the biomass of the higher trophic level was not reduced, whereas the biomass of low-trophic-level organisms increased. Like Raoux et al. (2017), Raoux et al. (2019), we consider this change as a restructuring of the community towards a new stable state rather than an unsustainable alteration of the ecosystem (Holling, 1996). We improved over Raoux et al. (2017), Raoux et al. (2019) by also observing a change in the ecosystem's functioning. This change was noticeable through the different responses of the BOWF and REEF models to climate change. When we impacted the two models with the climate change scenarios, very few similarities between the BOWF response and the REEF response emerged. The differences in the cascading responses to climate change between the BOWF and REEF models may be explained by a shift in the system (Andersen et al., 2009; Lees et al.,

2006). Our ENA results reflect a shift from a bentho-pelagic system towards a more benthic system. The system appeared more active with lower-trophic-level species relying less on herbivory and more on detritivory and recycling. Alongside the increase in redundant pathways, the system appeared more resistant to changes.

The ENA variations that we predicted between the BOWF model and the REEF model described a more resistant OWF system. Resistance is defined as the ability of a system to maintain its original state in a disturbed context as described by Holling (1996), and in accordance with 'ecological resilience' as described by Harrison (1979). Many ENA indices have been related to the notion of resistance. Lassalle et al. (2011) hypothesized that an increase in the detritivory to herbivory (D/H) rate was associated with a system more resistant to primary production variation. Recycling (FCI) may act as a buffer during disturbances and increase the resistance of the system (Saint-Béat et al., 2015). The overhead/redundancy of the flow (RoC and RoCi) may also act as a buffer during disturbances to maintain the system and thus increase its resistance (Ulanowicz and Norden, 1990). We predicted an increase of each of those indices (D/H, FCI, RoCi). Our results are less conflicting than the ones observed by Raoux et al. (2019) and describe a more coherent picture of the system, with benthic compartments playing a key role in the resistance of ecosystems (Norling and Kautsky, 2007; Dame and Christian, 2007; Raoux et al., 2019; Wang W., et al., 2019).

The effect of climate change on the system also appeared to validate the more resistant state of the REEF model, especially on the "fish, benthos feeders" scenario (FBF). The BOWF model led to more changes in ENA indices than the REEF model: Its lower omnivory level (SOI) revealed a less complex system evolving from a web-like system towards a more linear system (Libralato, 2013). As the complexity of a system is

an indicator of flexibility (Fagan, 1997; Lobry et al., 2008), we can expect a less stable and more vulnerable system. We also predicted that the system would lose part of its recycling capacity (FCI) and be less mature due to the lower redundancy of internal flows (RoCi) (Christensen, 1995; Odum, 1969; Ulanowicz, 2009; Ulanowicz and Norden, 1990). On the other hand, the only modeled effect of climate change on the "fish, benthos feeders" scenario of the REEF model was a higher detritivory to herbivory rate (D/H) of the system. As such, the reef effect seemed to increase the resistance of the system to climate change. However, one must not forget that these results depend on the way the climate change effect was modeled. The reef effect could also promote other effects of climate change, like the establishment of invasive species (Langhamer, 2012), but their study would need specific field experiments.

4.2. Role of the compartment impacted by climate change in the response of the ecosystem

Our analysis of the different ENA responses showed a pattern segregating the responses of the scenarios depending on the compartment impacted by climate change. The "fish, benthos feeders" (FBF) and the total (TOT) climate change scenarios showed important estimated changes in their structure and functioning, while the other climate change scenarios seemed close to their reference model. This happened in both the BOWF and REEF models. In both cases, the "fish, benthos feeders" (FBF) and the total (TOT) climate change scenarios impacted the "fish, benthos feeders" compartment (FBF). This leads us to think that the importance of the "fish, benthos feeders" compartment isn't defined by the aggregating role of the reef effect (Reubens et al., 2011), but rather by its position in the food web and thus its keystoneness. The keystoneness of a species defines its structuring role (Power et al., 1996; Libralato, 2019) and is not an intrinsic property of any given species (Fauth, 1999). The fact that the "fish, benthos feeders" compartment maintained its role despite the shift in the regime of the system might be due to the central position of its trophic niche in both systems.

The "fish, benthos feeders" (FBF) compartment seemed to play two roles in both models: first, it regulated the "invertebrates, benthic predators" compartment (IPR), and second, it ramified the system through its high omnivory. This was predicted when the "fish, benthos feeders" were impacted by the climate change effect (Fig. 7). The trophic niche of the "fish, benthos feeders" was thus claimed by the "invertebrate, benthic predators", and consequently changed the functioning of the food web. This result was different when considering the ecosystem shift caused by the reef effect: the "invertebrate, benthic predators" seemed more capable to replace the "fish, benthos feeders" in their niche. This replacement seemed to be facilitated by the shift of the ecosystem towards a more benthic system, in which the invertebrate benthic predators might be more successful in filling the same trophic role as the fish benthos feeders. As such, the system seemed less altered by the effect of climate change on the "fish, benthos feeders" scenario in the offshore wind farm system. However, we should remain careful because changing communities can have wider effects on the ecosystem likely to go undetected by trophic modeling approaches (Fontaine et al., 2011; Kéfi et al., 2015, 2012). As such, it is necessary to monitor such keystone species to maintain the ecosystem properties before, during and after the exploitation of the offshore wind farm. Previous studies have indeed already highlighted the advantages of monitoring keystone species (@@Payton et al., 2002; Libralato et al., 2006; Gelcich et al., 2010).

4.3. Understanding the mechanism behind the unexpected effect of the cumulative impact

Our scenarios show a wide variety of cumulative impacts, in line with previous studies that consider the additive effect to be the main type of combined effect in marine ecosystems, with a significant role of the cumulative impact on ecosystems (Crain et al., 2008). We evidenced synergetic and antagonistic effects, which proved the ability of ENA indices to reflect unexpected effects visible only when studying cumulative impacts (Jackson et al., 2001; Przeslawski et al., 2005). Cumulative impacts are often studied using community or population level metrics (Crain et al., 2008). By observing the same type of response with ENA, we demonstrate that cumulative effects are also significant at the functional level of the ecosystem. This is useful as it allows us to follow the properties of the ecosystem and its state in relation to the cumulated impact. Using functional metrics like ENA indicators might also help us better understand cumulative effects. This strengthens the importance of incorporating multiple scenarios of events in future ecological network analysis.

The strongest synergetic effect was predicted on the detritivory to herbivory (D/H) index of the "fish, benthos feeders" scenario (FBF). This synergistic effect seems to result from the shifting regime of the Courseulles-sur-Mer ecosystem. As the system shifted from a bentho-pelagic system to a more benthic system, the effect of climate change on the ecosystem functioning seemed to change (Fig. 7). In the BOWF model, the climate change effect on the fish benthos feeders resulted in an increased activity of the invertebrate benthic predators. This higher invertebrate benthic predator activity did not lead to an increase in detritivory because the system was not producing enough benthic detritus. Yet, this changed with the reef effect. As a system becomes more benthic, it produces more benthic detritus (Norling and Kautsky, 2008, 2007; Raoux et al., 2017). This increase in benthic detritus became available to the invertebrate benthic predators, and increased the detritivory to herbivory rate of the system. Many invertebrate benthic predators are indeed also scavengers. This changing response of the ecosystem to climate change due to the regime shift induced this unexpected effect on the detritivory to herbivory rate. This higher detritus consumption with the higher detritivory to herbivory rate of the OWF ecosystem resulted in a synergistic effect, as predicted by the "fish, benthos feeders" scenario (Table 2). An interaction between effects has already been shown to modify the effect of one or multiple events, e.g., in chemical reactions (Pelletier et al., 2006) and physiological/ecological reactions (Przeslawski et al., 2005; Christensen et al., 2006). We observed it at the functional level of the ecosystem. Integrating the evolving interactions between effects in a shifting ecosystem could help us better anticipate these effects. For us to detect those shifts, monitoring the entire ecosystem using ecological network analysis is needed, using local and relevant data on all trophic levels (Araignous et al., 2019).

While two effects can interact with each other toward a synergistic effect, they may also interact negatively, with a resulting antagonistic or dampened effect. This was mainly modelled for the detritivory to herbivory rate of the "flat fish" scenario (Table 2). When considered independently, the climate change effect and the reef effect increased the detritivory to herbivory rate. However, when the effects were combined, the cumulative effect on the detritivory to herbivory rate was dampened. This could be explained by the fact that the regime shift made the ecosystem impervious to the climate change effect. This mechanism of resistance has already been acknowledged at the physiological level or at the population level (Vinebrooke et al., 2004). ENA proved able to do the same at the functional level of the ecosystem.

The regime shift due to the reef effect seemed to explain multiple cumulative effects. However, sometimes it was uncertain whether the cumulated effect resulted from the model structure or not. This was visible on the total overhead of the "fish, benthos feeders" scenarios. In this case, the dominating effect of climate change overcame the cumulative effect (Table 2). With the "fish, benthos feeders" compartment relying significantly on imports (like cetaceous, seals and birds), a reduction of its biomass will lower the import overhead. As the import overhead is a part of the total overhead (Ulanowicz and Norden, 1990), the total overhead will decrease even though the internal overhead remains unchanged. This could be the result of the model structure itself, as the dependency of the "fish, benthos feeders" compartment to import

Table 2

Representation of the different mechanisms of the cumulative effects based on the LIM model results.

Scenario	ENA index	Climate change effect alone	Reef effect alone	Combined effects	Type of cumulative effect	Mechanism
Fish, benthos feeders (**FBF**)	Detritivory to herbivory (D/H)	+	+	+++	Positive synergistic	**Interaction** between the two effects due to the **regime shift** caused by the reef effect.
Fish, piscivorous (**FPI**)	Internal relative overhead (RoCi)	+	+	–	Negative antagonistic	**Interaction** between the two effects due to the **regime shift** caused by the reef effect.
Flat fish (**FFI**)	Detritivory to herbivory (D/H)	+	+	+	Positive dampened	**Resilience** of the ecosystem to the climate change effect due to the **regime shift** caused by the reef effect.
Fish, benthos feeders (**FBF**)	Relative overhead (RoC)	–	++	–	Negative antagonistic	The climate change effect **overpowers** the reef effect.

is mainly due to the reduced scale of the trophic model. Moreover, ENA indices are known to be potentially highly influenced by the model structure (Baird et al., 2009; Johnson et al., 2009). The lower import overhead could also be the sign of a more isolated system compared to the rest of the English Channel ecosystem (Baird and Ulanowicz, 1993).

4.4. Ecological network analysis indices: Sensitive tools to manage the cumulative impact of the REEF and climate change effects

Using a single ENA index to describe a changing system is not suitable to describe a changing ecosystem; a larger pool of indices is more adapted to reach an overall picture of the ecosystem organization and functioning (de la Vega et al., 2018). The same is true for combined impacts, which make it possible to predict different types of cumulative effects for different parameters of the ecosystem. While an index can describe a synergetic effect of the combined reef and climate change effects, another index may describe an antagonistic effect. This point should be emphasized when working on a limited number of indices, as multiple indices can be impacted differently. Interactions between events thus appear to be radiative – not unidirectional, i.e., different properties of an ecosystem can evolve in different ways. This emphasizes the need for complementary indices to provide a holistic view of the ecosystem (Fath et al., 2019; Safi et al., 2019), especially while addressing the effect of cumulative impacts.

Ecological network analysis indices seem to be suitable for addressing a wide range of cumulative effects. Along with an integrative approach, this ability to study cumulative impacts in their overall diversity makes ENA indices the ideal ecological indicators necessary for the future of ecological science and management (de la Vega et al., 2018; Fath et al., 2019; Safi et al., 2019). It is now time to implement those indices in more complex cumulative impact scenarios to describe the mechanisms behind cumulative impacts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107128.

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