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An ecosystem-wide approach for assessing the spatialized cumulative effects of local and global changes on coastal ecosystem functioning

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Coastal ecosystems are subjected to an increasing number of anthropogenic drivers, including marine renewable energies and climate change (CC). These drivers can interact in complex ways, which may lead to cumulative effects (CEs) whose potential consequences on the ecosystems need to be addressed. We used a holistic approach—ecological network analysis (ENA)—coupled with a two-dimensional food web model—Ecospace—to conduct an ecosystem study of the CEs of CC plus the operation of an offshore wind farm on ecosystem functioning in the extended Bay of Seine (English Channel). Mapped ENA indices showed that CEs were not restricted to the wind farm area, i.e. where anthropogenic drivers are concomitant. CEs varied both in space and among ecosystem properties, displaying that ENA indices can distinguish between different cumulative pathways that modify ecosystem functioning in multiple ways. Moreover, the effects seemed to be tied to the structuring role of CC, and differed under the 2050 and 2100 conditions. Such changes resulted in stronger loss of ecosystem resilience under the 2100 conditions despite the benefits of the reef and reserve effects of the wind farm.

Keywords: climate change, coastal ecology, combined drivers, cumulative effects, ecological network analysis, ecosystem functioning, fishing, offshore wind farm, resilience.

Highlights

- Interactions between offshore wind farms and climate change (CC) can lead to a wide range of CE on ecosystems regardless of fishing activities.
- The structuring role of CC seems to have a predominant role in the formation of cumulative effects (CEs).
- CEs appear heterogeneous across space, over time and among ecosystem functional properties.
- In 2050, the combined effects of CC and the wind farm remain positive for ecological resilience.
- In 2100, interactions between CC and the wind farm change, reducing ecological resilience.

Introduction

When multiple anthropogenic drivers—fishing and climate change (CC) among others—co-occur in an ecosystem, they often interact with each other to produce cumulative effects (CEs) on the ecosystems (Folt and Chen, 1999; Vinebrooke *et al.*, 2004). CEs have been observed in many marine ecosystems (Crain *et al.*, 2008; Halpern and Fujita, 2013). They can result in different ecosystem changes than the sum of the individual drivers, that can be synergistic, antagonistic, or damp-

ened. These interactive effects occur at all the levels of biological organization, from single organisms to complex and interconnected systems (Stelzenmüller *et al.*, 2018). In ecosystems, CEs result from complex interactions among ecosystem drivers and depend on ecosystem functioning (Breitburg *et al.*, 1998; Boyd and Hutchins, 2012). They can emerge through interactions within the food web, via trophic cascading. In a world subjected to intense human activities and CC (IPCC, 2021), understanding the effect of each individual driver is not enough. Interactions among drivers in ecosystems must also be studied because they could represent a major threat for marine conservation and management (Willsteed *et al.*, 2017; Gissi *et al.*, 2021).

It is important to understand the full extent to which biotic and abiotic drivers affect ecosystems to properly manage marine resources (Rombouts *et al.*, 2013; Heymans *et al.*, 2020) and where these effects take place (Halpern and Fujita, 2013). The European marine spatial planning directive (2014/89/EU) requests EU members to establish spatial planning processes to achieve ecological, economic, and social development. Ecosystem-based management has been advocated as a key pillar for the sustainable management of marine and coastal environments (Langlet and Rayfuse, 2018). As a re-

sult, CEs on the whole ecosystem functioning must be considered across time and space to manage ecosystems efficiently. This would ensure more accurate spatial zoning decisions and ecosystem-based management plans (Buhl-Mortensen *et al.*, 2017; Le Tissier, 2020). Unfortunately, time passed until CEs were properly considered in strategic environmental impact assessment (Bidstrup *et al.*, 2016), and there is still an urgent need to further include them nowadays (Guşatu *et al.*, 2021).

Spatial cumulative assessment studies often fail to explore the complex nature of CEs because (i) interactions among ecosystem components and drivers are frequently ignored, and CEs are considered additive, and (ii) each driver is usually mapped using the expected footprint of an impact, without considering the specific response of habitat/community types to the tested drivers (Ban *et al.*, 2010; Halpern and Fujita, 2013; Kotta *et al.*, 2020; Guşatu *et al.*, 2021).

Mapping the expected environmental footprints of multiple anthropogenic drivers can help identify areas prone to cumulative impacts and possibly requiring thorough monitoring to limit CEs; but using expert judgement does not allow for an accurate representation of the ecosystem processes that pilot interactions among drivers like trophic interactions. Such complex processes depend on many ecosystem parameters [ecosystem heterogeneity, species tolerances, displacement, and driver magnitude among others (Vinebrooke *et al.*, 2004; Boyd and Hutchins, 2012)], and may affect the spatial extent of CEs and in turn the areas subjected to cumulative responses. The assessment of spatial CEs would greatly benefit from ecosystem approaches taking the complexity of the food web into account to represent the mechanisms leading to CEs (both direct and indirect). It would ensure a quantitative assessment of CEs and their impacts on ecosystem functioning to monitor ecosystems more efficiently (Buhl-Mortensen *et al.*, 2017; Le Tissier, 2020). With their shared vision of ecosystems as networks of interactions, cumulative assessment methods, and ecosystem approaches seem to fit together to build a coherent tool for marine management and zoning purposes.

Ecological network analysis (ENA) indices can be used to link both ecosystem approaches and cumulative assessment. ENA indices are utilized to understand the functioning of a food web; they provide an integrative and holistic view of ecosystem functioning, organization, and structure (Ulanowicz, 1986; Baird and Ulanowicz, 1993; Borrett and Scharler, 2019). ENA indices can be computed using food web modeling techniques and have been extensively promoted as promising tools for ecosystem-based management (Ulrike *et al.*, 2018; Fath *et al.*, 2019; Safi *et al.*, 2019). They have already been used to study the CEs and the spatial effects of multiple individual anthropogenic drivers (Nogues *et al.*, 2020; Nogues *et al.*, 2022).

Ecopath with Ecosim (EwE) is a food web modelling framework that can explore cumulative impacts on ENA indices (Christensen and Walters, 2004). The spatialized version of Ecopath—Ecospace—was used in Nogues *et al.* (2022) to compute maps of ENA indices in order to understand the spatial organization and functioning of the extended Bay of Seine ecosystem (eBoS, English Channel). Based on its functioning, the Bay of Seine was divided into multiple five functional regions (Nogues *et al.*, 2022). These five regions were used to characterize the potential individual effects of multiple drivers using ENA indices. These drivers included the potential effects of CC on species distribution and the exploitation of the off-

shore wind farm (OWF) of Courseulles-sur-Mer (in the Bay of Seine) under varying fishing efforts.

In this study and in continuity of the approaches of Nogues *et al.* (2022), we combined the different drivers previously modelled in the eBoS model to evaluate holistically how their effects could affect the organization and the functioning of the eBoS ecosystem. We aimed to characterize the mechanisms that drive CEs as well as the locations where ecosystem functioning was mostly impacted by CEs. Finally, we studied the effects of the combined drivers on the resilience of the ecosystem.

Materials and methods

Study area

The eBoS Ecospace model covers the coastal ecosystem of the Bay of Seine, from the Cotentin Peninsula to Le Havre and from the French coastline to the French–British delimitation of the exclusive economic zones (Figure 1). It is a shallow coastal ecosystem open onto the English Channel in the north, with depth varying from 5 to 70 m in the Paleo-valley of the Seine (mean 35 m). It covers 13500 km^2 and is mainly composed of gravel and coarse sand in the offshore part of the bay, while fine sand and muddy fine sand are located near the coast (Dauvin, 2015). This area is heavily anthropized and is home to many human activities including fishing, aggregate extraction, marine renewable energy, tourism, fret transport, and pleasure sailing among others (Dauvin, 2019).

In Nogues *et al.* (2022), the eBoS was divided into five functional regions to help distinguish the effects of the different anthropogenic drivers on the ecosystem. A K-means clustering analysis (MacQueen, 1967) was performed on ecological indicators of the reference model (Supplementary materials 1 Figure S1–1) to determine functional regions. Three regions with different properties of functioning were defined (Nogues *et al.*, 2022) and named "Coastal Bay of Seine" (CBoS), "Offshore Bay of Seine" (OBoS), and "Central English Channel" (EC) from coast to offshore. These regions clearly depicted a coast-to-offshore gradient, with the most coastal region more resilient and complex and the farther regions less so. We defined two other structural regions based on the OWF of Courseulles-sur-Mer inside the CBoS functional region and named them "Offshore wind farm" (OWF) and "Spillover region" (Spill). All the regions were mutually exclusive (Figure 1).

Ecospace spatialized food web modeling

The eBos food web was modelled with a modified version of Ecopath with Ecosim (*EwE* 6) software (Pauly *et al.*, 2000). This software can be used to model marine food webs: in a static way with Ecopath (Pauly *et al.*, 2000), in a time-dynamic way with Ecosim (Christensen and Walters, 2004), and in a temporal-spatial way with Ecospace (Walters *et al.*, 1999; Christensen *et al.*, 2014). The *EwE* 6 version we used was specially modified to compute food web indices (Nogues *et al.*, 2022). Following Nogues *et al.* (2022), this study is based on Halouani *et al.* (2020) to model the eBoS ecosystem (Figure 2a).

The original eBoS Ecopath was composed of 42 groups, including 40 living groups with a wide variety of marine species—from phytoplankton and bacteria to bottlenose dolphins and sea birds—and two non-living groups; detritus
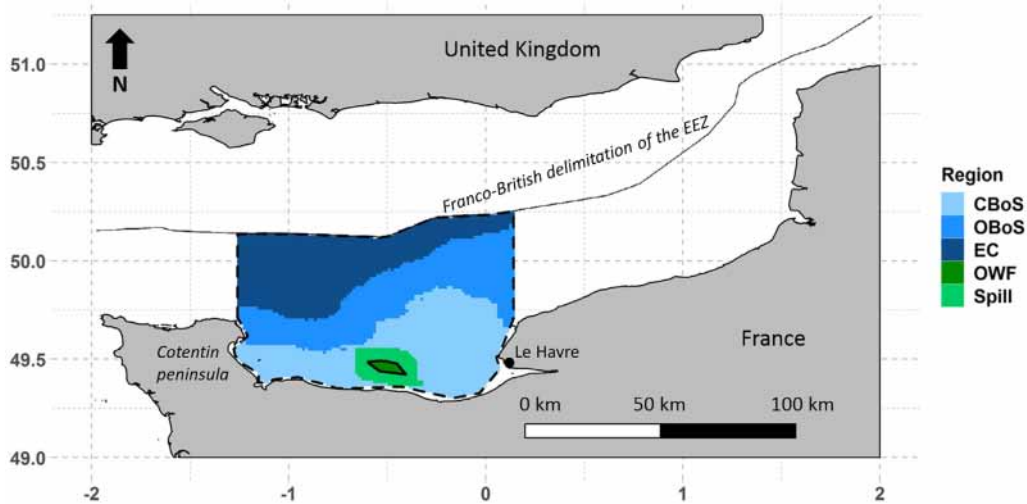
Figure 1. Map of the eastern part of the English Channel and location of the eBoS Ecospace model. The Ecospace model was divided into five regions: CBoS, OBoS, and EC (Central English Channel), OWF, and Spill (Spillover region surrounding the OWF). All regions are exclusive.

and discards (Supplementary materials 1 Table S1–1). This Ecopath model served as a basis to build an Ecosim time-dynamic model using 21-time series of catches (IFREMER SIH, 2017) and eight-time series of biomass from multiple stock assessment surveys (2000–2015) (Halouani et al., 2020). An Ecospace model was later built to spatially model the eBoS ecosystem. The eBoS model map was composed of 4907 cells with a resolution of 0.015° × 0.015°, and each cell modelled a time-dynamic Ecosim food web. Species distributions inside the eBoS Ecospace model were driven using a depth map from the General Bathymetric Chart of the Oceans (https://www.gebco.net/), a primary production map from SeaWifs representing the relative chlorophyll a concentration in the bay in 2000 (https://podaac.jpl.nasa.gov/), and multiple environmental driver maps for 27 of the 40 trophic groups (Supplementary materials 1 Tables S1–1 to S1–3; Figures S1–2 to S1–36; Halouani et al., 2020; Bourdaud et al., 2021; Nogues et al., 2022). Environmental driver maps were built from suitability index maps computed from niche models by Ben Rais Lasram et al. (2020) and were used to define habitat suitability for the specified species (Christensen et al., 2014). Suitability index maps were computed using 2005–2012 climate and habitat parameters (temperature, salinity, type of substrate, depth, seafloor slope, and orientation to the north). All the parameters of the eBoS model are available in Halouani et al. (2020), Bourdaud et al. (2021), and Nogues et al. (2022).

Modeling of anthropogenic drivers: effects of CC the OWF of courseulles-sur-mer and fishing

We focused on two main anthropogenic drivers in the eBoS Ecospace model (Nogues et al., 2022): CC and the operation of an OWF.

To model the effects of CC, the spatio-temporal framework of *EwE* (Steenbeek et al., 2013) was used. This Ecospace tool can modify Ecospace inputs over time, such as environmental driver maps. In the present study, it was used to replace the initial suitability index maps computed from 2005 to 2012 climate parameters of the baseline eBoS Ecospace model, with new suitability index maps simulating the effects of CC on species distribution (Nogues et al., 2022). Two conditions were tested—using two new sets of suitabil-

ity index maps computed at two different horizons (2050 and 2100)—of the IPCC "business as usual" CC projection (RCP 8.5, considered the most likely scenario; Schwalm et al., 2020). One condition represented the 2050 decade (2041–2050), while another represented the 2100 decade (2091–2100) (Nogues et al., 2022; Figure 2). By replacing the reference "current" suitability index maps of the baseline eBoS model during the Ecospace model run, with either the 2050 or the 2100 condition suitability index maps, we changed the habitat suitability for the eBoS trophic groups according to the effect of CC on their suitability. After replacing the suitability index for each CC condition (2050 and 2100), the Ecospace model was run to equilibrium. In doing so, CC-induced changes to the environmental parameters that affected the habitat suitability of the impacted groups in Ecospace. Following the foraging arena theory (Walters et al., 1997, 1999), changes in habitat suitability affect consumption by the groups in the cells and modify their production and biomass and thus their distribution and dynamic (Christensen et al., 2014).

The long-lasting effects of the future OWF of Courseulles-sur-Mer were modelled following previous works including Halouani et al. (2020) who first modelled the reserve effect of the OWF. We improved on Halouani et al. (2020): by modelling a limited closure of the farm following the owners' proposal to "optimize" fishing inside the farm (~15%, Raoux et al., 2018, 2019) and by modelling the potential reef effect of the OWF (Nogues et al., 2022). The reef effect was simulated based on Raoux et al. (2017), which used Ecosim to simulate the introduction of new hard substrates to the Courseulles-sur-Mer ecosystem (Figure 2a). Using the spatial-temporal framework of *EwE* (Steenbeek et al., 2013), biomass changes observed in Raoux et al. (2017) due to the reef effect were transposed to new environmental driver maps to increase the habitat suitability of multiple benthic and demersal groups inside the OWF (Table 1 and Supplementary materials 1 Tables S1–4; Nogues et al., 2022). Combined with the 15% closure to fishing, this means that this study focuses on both the reef and the reserve effects of the OWF, two effects considered as highly structuring on the ecosystems (Langhamer, 2012; De Mesel et al., 2015).
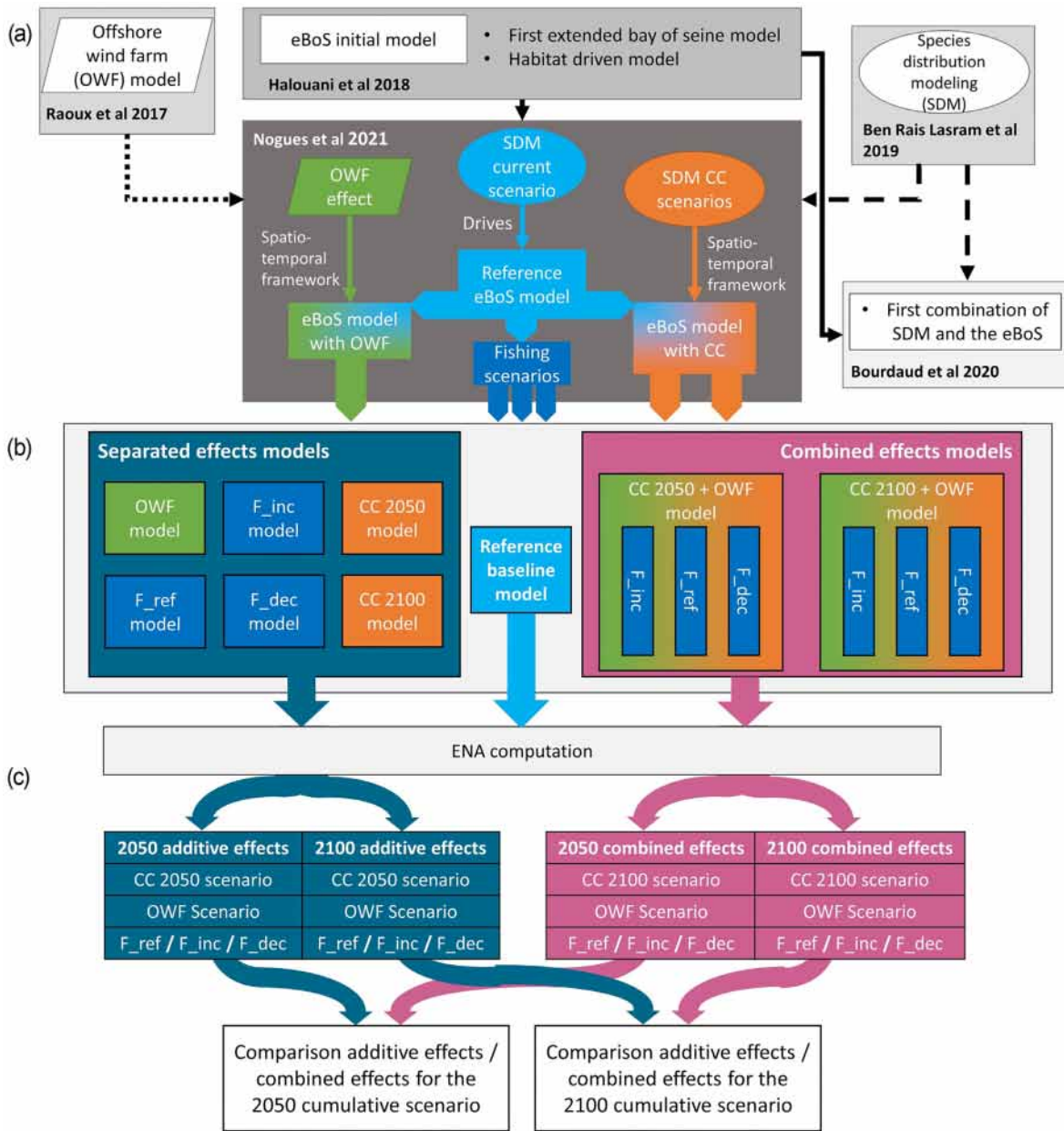
Figure 2. Diagram of the modelling framework. Describes vertically: (a) previous work leading up to this study and their relationships (solid: same model; dashed: same approach; and dotted: used data), (b) the modelling framework used in this study, and (c) the CEs assessment procedure.

Table 1. Value of the environmental drivers used in Ecospace to model the reef effect on the habitat suitability of the eBoS trophic groups based on Raoux *et al.* (2017).

OWF presence	eBoS groups	Ecospace reef environmental driver
No	All	1.00
Yes	Surface feeders seabirds	6.11
Yes	Fish Atlantic cod	3.49
Yes	Fish whiting	4.18
Yes	Fish pouting	2.32
Yes	Fish benthos feeders	2.07
Yes	Fish sole	1.93
Yes	Fish flounder	4.37
Yes	Fish dab	4.37
Yes	Benthic inv. predators	1.02
Yes	Benthic inv. filter feeders	1.53
Yes	Benthic inv. bivalves	2.20

Table 2. ENA indices computed with EnaR from Ecospace SCOR files (see Supplementary materials Table S–8 for formulas).

Name	Objective	References
Relative flow redundancy (RDC)	Quantify the relative redundancy of the flows in the system.	Ulanowicz and Norden (1990) and Christensen (1995)
System omnivory (SOI)	Determine the level of omnivory of the system, i.e. to what extent the groups in the system consume multiple other groups.	Libralato (2013)
Finn cycling index (FCI)	Specify how much energy of the system passes through cycles.	Finn (1980)
Mean trophic level (MTL 2)	Quantify the mean trophic level of the system and thus the ecological community structure.	Latham (2006)

In Nogues *et al.* (2022), three fishing scenarios based on the potential effect of Brexit on fishing were tested. These scenarios either decreased or increased the fishing effort of trawls and other gears and decreased dredge effort (Supplementary materials 1 Tables S1–5 to S1–7). They were built to simulate the potential effect of Brexit on fishing in the area. These scenarios had negligible effects on the ecosystem (Nogues *et al.*, 2022) and preliminary results showed that when combined with CC and the OWF, there was little difference in the cumulative response between fishing scenarios (Supplementary materials 2 Figures S2–17 to S2–32). Therefore, we did not consider fishing scenarios explicitly in the assessment of CEs. Instead, all fishing scenarios were combined with each other to build two cumulative scenarios, combining the effect of the OWF and of CC under the 2050 and 2100 conditions. These two cumulative scenarios were designed to study the combined effects of CC and the OWF while considering potential fishing variations in the eBoS. They were called "Combined 2050" and "Combined 2100:

Combined 2050: CC 2050 + the OWF with each fishing scenario (F_ref, F_inc and F_red).

Combined 2100: CC 2100 + the OWF with each fishing scenario (F_ref, F_inc and F_red).

Ecological network analysis

The scenarios built in Nogues *et al.* (2022) were used to compute maps of ENA indices using the "EnaR" Ecospace plugin (Nogues *et al.*, 2022). This plugin available in a modified version of *EwE* 6 is used to create Scientific Committee for Ocean Research (SCOR) formatted files for each cell of the Ecospace model at each time step. SCOR files contain all the data needed to create maps of ENA indices using the R package "EnaR" (Borrett and Lau, 2014). Each cell of the Ecospace model had ENA values that were used to build ENA maps using the same resolution as Ecospace (Supplementary materials 1 Figure S1–1). We selected four ENA indices to describe and understand the functioning and organization of the food web (Table 2), based on previous lists of ENA indices considered promising for ecosystem management due to their insights into ecosystem functioning and ecosystem resilience (Fath *et al.*, 2019; Safi *et al.*, 2019). Each cumulative scenario had three sets of ENA results—one *per* fishing scenario.

Assessment of CEs

ENA indices can assess the CEs on the ecosystem properties, as described in Nogues *et al.* (2020). The methodology of Travers-Trolet *et al.* (2014) and Fu *et al.* (2018) was applied to determine the type of CE. This method considers that CEs can be synergistic, antagonistic, or dampened. It also consid-

ers the direction of the effect on the studied index (positive or negative relative to the reference).

To determine CEs, we computed the relative index change (delta) between the reference scenario and each independent driver [Equation 1, e.g. the OWF alone or one of the CC conditions (2050 or 2100) or one of the fishing scenarios] for all ENA indices.

$$\Delta I_s^{sep} = \frac{I_s - I_r}{I_r},\qquad(1)$$

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).

Then, we summed the ΔI_s^{sep} of each driver (CC, OWF and fishing) for each combination (F_red, F_inc, and F_ref) in each cumulative scenario (cumulative 2050 and cumulative 2100, Figure 2b and c). This yielded three additive effects $\sum \Delta I_s^{sep}$ *per* cumulative scenario ($\sum \Delta I_s^{sep}$F_red, the $\sum \Delta I_s^{sep}$F_inc and the $\sum \Delta I_s^{sep}$F_ref). To characterize CEs, we compared the three additive effects ($\sum \Delta I_s^{sep}$F_red and $\sum \Delta I_s^{sep}$F_inc and $\sum \Delta I_s^{sep}$F_ref) to the three corresponding combined effects (ΔI_c^{cum}F_red and ΔI_c^{cum}F_inc and ΔI_c^{cum}F_ref), (Figure 3, Equation 2) for the 2050 and 2100 cumulative scenarios.

$$\Delta I_c^{cum} = \frac{I_c - I_r}{I_r},\qquad(2)$$

where I_r is the index value of the reference model and I_c the index value of the combined drivers (CC effects + OWF effects + one fishing scenario).

Comparison of additive effects and combined effects

To assess CEs, the additive effects were compared to the combined effects. The CEs under the 2050 and the 2100 cumulative scenarios were determined using two methods. First, the effects were determined for each region (functional and structural) of the eBoS (Figure 1) by comparing the average additive effect ($\overline{\sum \Delta I_s^{sep}}$ averaging each combination *per* cumulative scenario) with the average combined effect ($\overline{\Delta I_c^{cum}}$ averaging each combination *per* cumulative scenario) under each cumulative scenario, using barplots. If the two averaged effects ($\overline{\sum \Delta I_s^{sep}}$ and $\overline{\Delta I_c^{cum}}$) were equal, we considered that no CE resulted from the combined drivers (Figure 3, case 1), and if there was differences, than there was CEs (Figure 3).

The Cliff delta (Cliff, 1993; Tecchio *et al.*, 2016) effect size metric was also used to compare the additive effect and the combined effect for each cumulative scenario (Cumulative 2050 and 2100) in each cell of the eBoS Ecospace model (4907 comparisons). It was chosen because it is a non-parametric effect-size metric that can be used to compare datasets with

Figure 3. Comparison of the additive and combined effects of drivers to determine the resulting cumulative effect of drivers on ENA indices. Case 1: no cumulative effect; case 2: positive dampened; case 3: positive synergistic; case 4: negative synergistic; case 5: negative dampened; case 6: positive antagonistic; and case 7: negative antagonistic.

different treatments. The Cliff delta determined if the difference between the $\sum \Delta I_s^{sep}$ and the ΔI_c^{cum} (*per* cumulative scenario) was large, medium, small, or negligible. If the difference was considered large, based on the threshold given by Romano *et al.* (2006) (| ∂Cliff | < 0.474), then the CE was considered significant in the cell. This allowed a more precise discrimination of CEs within the eBoS and enabled the mapping of CEs despite variability inside the regions and between fishing scenarios.

In Ecospace, the habitat suitability drives the distribution and dynamic of trophic groups. It is the product of the group responses to each environmental driver: here CC and to the OWF reef effect. Due to the fact that the habitat suitability is a product, the relative effects of CC and the OWF on the suitability are constant, but can have different absolute effects. Let's take for example two drivers, A and B, with a response of 0.5 and 0.1, respectively, in the reference model. If driver B's response increases to 0.6, then the group capacity will increase to 0.3, a 500% increase compare to the reference. If, on the other hand, driver A's response is increased simultaneously to 0.8, then the habitat capacity will increase to 0.48. While this will still result in a 500% increase of the habitat capacity, the absolute increase of the habitat capacity will be different due to driver A (a 0.25 increase in the first case and a 0.4 increase in the second case). Compared to the reference, the combine effect of drive A and B will thus have a higher absolute effect than each effect taken separately. This difference in the absolute effect of the drivers on the habitat suitability is akin to a cumulative response, where the intensity of one driver may impact the intensity of another. In this case, however, this is governed by the Ecospace equations. To determine what are the consequences of the habitat suitability model on CEs, the same cumulative assessment method was used to distinguish CEs on the habitat suitability and on the biomass of the different groups. This assessment was made by combining the effect of CC in both conditions (2050 and 2100) and the reef effect of the OWF.

Results

CEs in the eBoS regions

The graphical comparison of the additive and combined effects under the two cumulative scenarios (combined 2050 and combined 2100; Figure 4) showed that only the OWF appeared to be affected by CEs. This was similar to what is observed on the habitat capacity. Out of the 10 groups displaying CE on their habitat capacity, four and five displayed different CEs on their biomass, with greater differences in 2100 (Table 3). Moreover, all 40 groups appeared to show CEs on their biomass.

The average additive effect was an outlier to the average combined effect for the recycling index (FCI), the mean trophic level (MTL2), and relative flow redundancy (RDC), despite variability (i) inside the OWF sub-region and (ii) among the three fishing scenarios within each cumulative scenario (Figure 4). Under the 2050 cumulative scenario, CEs inside the OWF were always positive—positive synergistic for the FCI and positive dampened for the MTL2 and RDC. Under the 2100 cumulative scenario, CEs within the OWF were similar to those under the 2050 cumulative scenario for FCI and MTL2–positive synergistic for the FCI and dampened positive for the MTL2 (Figure 4). However, a negative CE—negative synergistic for relative redundancy (RDC, Figure 4)—was found under the 2100 cumulative scenario that was not found under the 2050 cumulative scenario. Another region that seemed to exhibit a CE was the Spillover region under the 2050 cumulative scenario, for the system omnivory (SOI). However, this effect was not as clear-cut as in the OWF region because there was greater variability within the region.

Red colour indicates the degree of difference between CE (different CE with same direction < opposite CE direction). Abbreviations include: positive (pos.), negative (neg.), and invertebrate (inv.).
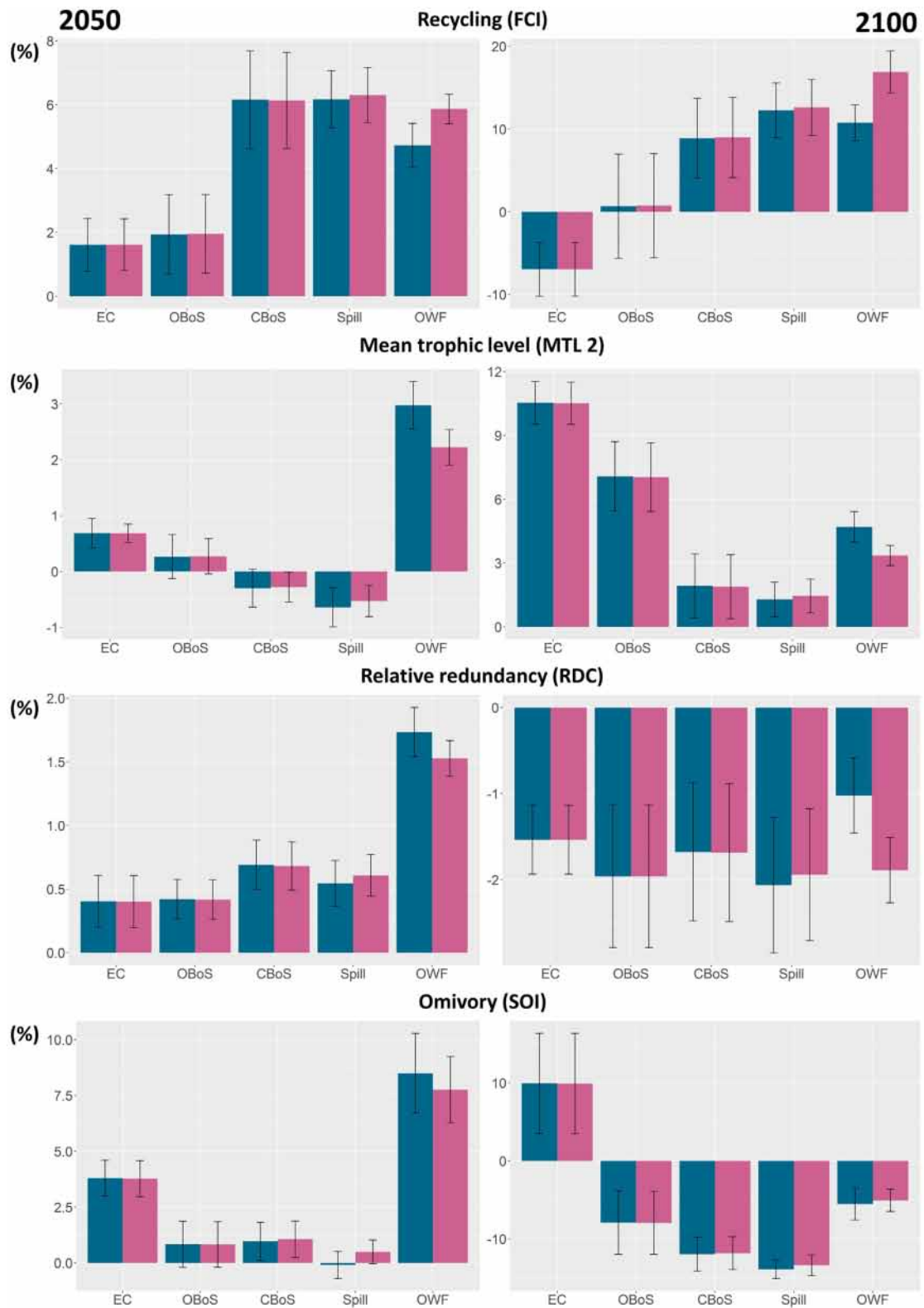
Figure 4. Regional differences in % between the averaged additive effect (blue) and the averaged combined effect (red) under the two cumulative scenarios (2050 left column and 2100 right column). Regions include: English Channel (EC); OBoS; CBoS; Spillover (Spill); and OWF. The standard deviation for the cumulative scenario was calculated with the values of all the cells of the given region, for all the combinations of drivers (F_ref, F_inc, and F_red), and was pictured with error bars. Error bars show the standard deviations within the regions and among the driver combinations under each cumulative scenario.

Table 3. Comparison between the CEs visible on the habitat capacity and on the biomass of the groups in 2050 and 2100.

eBoS groups	2050		2100	
	CE in habitat capacity	CE in biomass	CE in habitat capacity	CE in biomass
Fish Atlantic cod	Dampened pos.	Dampened pos.	Antagonistic neg.	Antagonistic neg.
Fish whiting	Dampened pos.	Dampened pos.	Antagonistic neg.	Antagonistic neg.
Fish pouting	Dampened pos.	Synergistic pos.	Antagonistic neg.	Synergistic neg.
Fish benthos feeders	Dampened pos.	Synergistic pos.	Antagonistic neg.	Synergistic pos.
Fish sole	Dampened pos.	Synergistic pos.	Dampened pos.	Synergistic pos.
Fish flounder	Dampened pos.	Dampened pos.	Antagonistic neg.	Antagonistic neg.
Fish limande	Antagonistic neg.	Antagonistic neg.	Antagonistic neg.	Antagonistic neg.
Benthic inv. predators	Synergistic neg.	Synergistic neg.	Synergistic neg.	Synergistic pos.
Benthic inv. filter feeders	Dampened pos.	Dampened pos.	Synergistic neg.	Synergistic neg.
Benthic inv. bivalves	Dampened pos.	Synergistic pos.	Antagonistic neg.	Synergistic neg.

Spatial CEs

CEs were spatially closely linked with the OWF, with varying sensitivity of the indices and scenarios. The MTL2 was the only index that displayed CEs far outside the OWF region, in all the regions of the model. Even though a lot of cells showed CEs, they were mixed (positive synergistic with positive dampened, negative synergistic with negative dampened), resulting in the absence of visible CEs at the regional scale (Figure 4) despite the large amplitude of the effects.

The OWF region consistently displayed most of the CEs in the eBoS, but results at the cell level showed that CEs could also occur elsewhere (Figure 5). The OWF region displayed uniform CEs. The Spillover region showed intra-regional variability of CEs, especially under the 2050 scenario, with a uniform positive synergistic effect on the FCI and RDC, but heterogeneous effects on the SOI—positive synergistic, positive antagonistic, and negative dampened effects all mixed together across the region (Figure 5). Under the 2100 scenario, CEs were more homogeneous across the region. This trend was not just visible at the regional scale: CEs were altogether more homogeneous under the 2100 scenario than under the 2050 scenario (Figures 5 and 6).

CEs in both scenarios varied according to ENA indices (Figures 5 and 6). Both scenarios displayed a similar positive synergistic effect within and around the OWF for the FCI, but the SOI and RDC had different CEs under each scenario, with positive effects under the 2050 scenario and negative ones under the 2100 scenario. The effects under the 2100 scenario were also higher than the effects under the 2050 scenario: CEs had a 5% positive synergistic effect on the FCI in the OWF sub-region under the 2100 scenario, vs. a 2% synergistic increase of the FCI under the 2050 scenario (Figures 5 and 6).

Discussion

This study proposed an innovative method to characterize CEs on the functioning of an ecosystem using holistic indices. However, we must consider the limitations of the approach. First, we did not account for the explicit role of fishing as our fishing scenarios were not substantial enough to have significant effects on the ecosystem (see Nogues *et al.* 2022). Understanding the relationships between fishing and CC is indeed a priority (Gissi *et al.*, 2021). Both may have strong interactions and could lead to significant changes to marine ecosystem (Ainsworth *et al.*, 2011). Unfortunately, our fishing scenarios did not enable us to do

so directly, but rather through the consideration of fishing variability.

Other limitations include the one detrimental to Ecopath, which were discussed in Christensen and Walters (2004) and Ainsworth and Walters (2015). Some of these limitations may limit our ability to model CC like the inability to take into account environmental drivers variability or the constant physiological ratios of trophic groups in Ecospace. CC modelling would greatly benefit from the ability to take species adaptation into account (Hoffmann and Sgró, 2011) as well as to better integrate input variability. Other benefits would be to consider the arrival of non-indigenous species in the system (Corrales *et al.*, 2018; Le Marchand *et al.*, 2020). These limitations were not resolved in this study due to methodological reasons, in order to keep the number of scenarios as small as possible, to facilitate CE assessment (Nogues *et al.*, 2022). Despite these limitations, studying CEs on whole ecosystem functioning remains a priority often overlooked when using ecosystem approaches, even though such ecosystem approaches are increasingly used (Gissi *et al.*, 2021).

Mapping of CEs using ecosystem approaches

CEs mainly occurred within the OWF region, where both anthropogenic drivers—CC and the OWF—coincide. This was mainly visible inside the OWF region, where the differences between the habitat capacity of the separate and combined effects were observed. However, CEs were not only visible on the species impacted by both drivers, but on the functioning and structure of the entire ecosystem. Multiple ecosystem indices showed this, including the recycling (FCI), the mean trophic level of the consumers (MTL2), and the relative redundancy of the flows (RDC). This further confirmed the importance of considering larger-scale drivers like CC when assessing the environmental impact of local strategic activities (Willsteed *et al.*, 2017). Indeed, local and global drivers may interact with each other through trophic cascading, leading to unsuspected consequences on the ecosystem at the local scale (Brown *et al.*, 2013). Even at the trophic group scale, when the habitat capacity model predicted one type of cumulative response, the CE visible on the biomass of the group was different due to trophic relationships with other groups. This highlights the importance of considering the combined effects of local and global drivers on complex systems such as food webs (Boyd and Hutchins, 2012; Nogues *et al.*, 2021), whether in space or in the system itself.

CEs were important across the OWF region, but it was not the only region with noticeable effects. They were also vis-
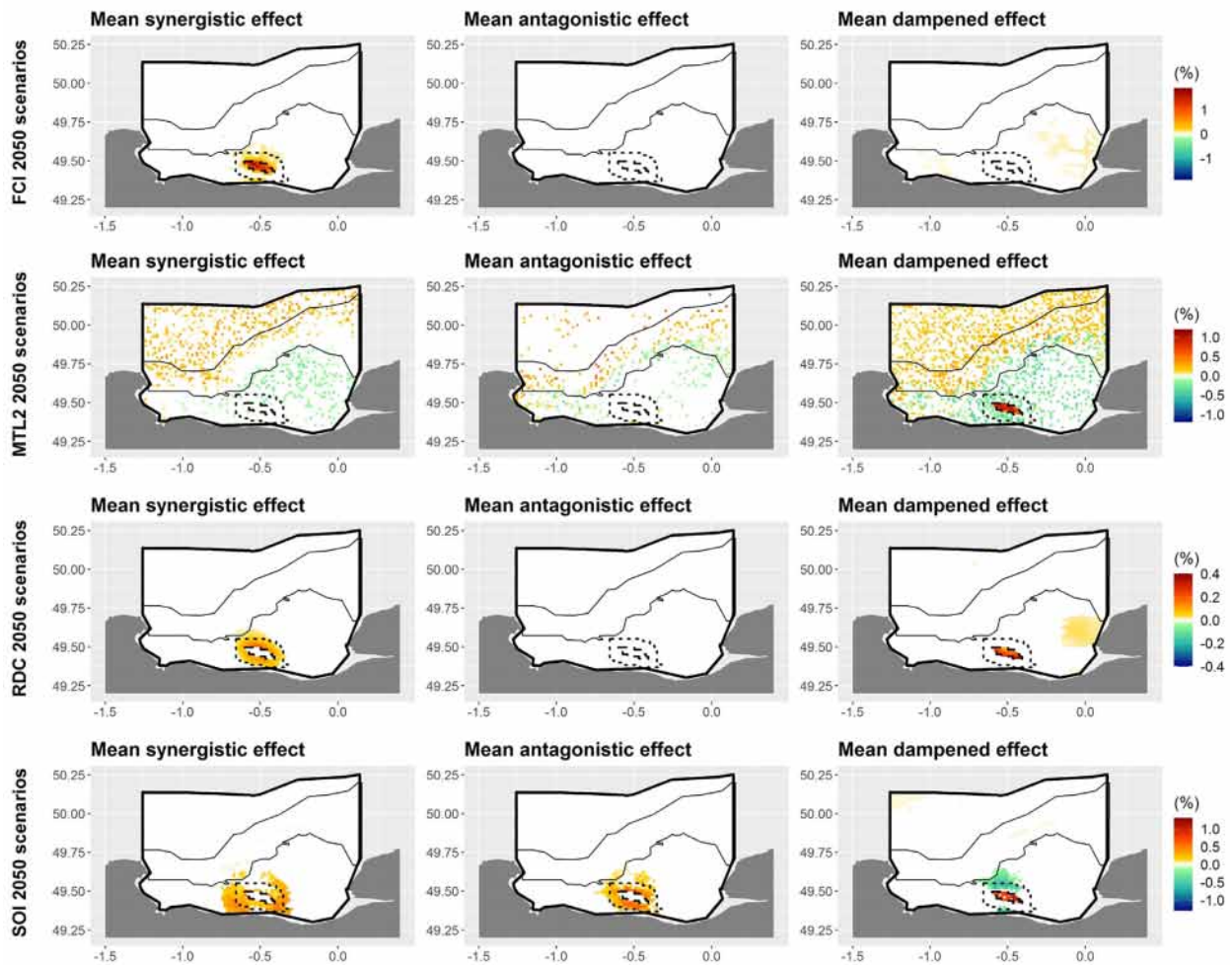
Figure 5. Strong CEs under the 2050 cumulative scenario according to the Cliff delta metric. The averaged CEs were mapped when the difference between the additive effect and the combined effect was considered large by the Cliff delta. Maps were sorted *per* row (ENA indices) and *per* column (cumulative effect). Warm colours, positive CEs relative to the reference model; cold colours, negative CEs relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.

ible in multiple cells outside the OWF region—regions that did not display CE on the habitat capacity—such as in the spillover region surrounding the farm and the coastal region. Moreover, the extent of these effects differed among ENA indices, with heterogeneous CEs inside and outside the OWF region. The varying CEs *per* ENA index, already observed by Nogues *et al.* (2020), indicated that CEs can differ depending on the ecosystem property, and that CEs result from different trophic relationships which can be related to multiple cumulative pathways (Spaling, 1994). A cumulative impact may affect differently each species of an ecosystem (Fu *et al.*, 2018; Ortega-Cisneros *et al.*, 2018), and the same goes for ecosystem properties (e.g. recycling, omnivory, or flow redundancy). For example, CEs on flow redundancy may be linked to simultaneous changes at multiple trophic levels, which can result in a different CE on the SOI. As habitat and ecological communities are not homogeneous in space and ecological responses to drivers differ among trophic groups (Schiel *et al.*, 2014; Epstein and Smale, 2018), such coordination may vary across space. Moreover, trophic groups may not move at the same rate in the ecosystem. Therefore, ecosystem responses to multiple drivers should not be generalized: Two given drivers may interact differently in different ecosystems (Cocklin *et al.*,

1992; Gissi *et al.*, 2021) and may not interact uniformly within a given ecosystem. Current cumulative assessment works often overlook such variability (Ban *et al.*, 2010; Halpern and Fujita, 2013; Kotta *et al.*, 2020). Therefore, ecosystem approaches should be promoted to model these structures and properly assess the multiple effects of combined drivers on the ecosystem. This could also greatly help the mapping of the potential interactions between two large-scale drivers like fishing and CC because they may have complex spatial patterns of CEs depending on ecosystem heterogeneity that conventional CE assessment may not be able to grasp.

CEs and CC

Ecosystem approaches also benefit from their ability to detect potential ecosystem restructuring, which plays a key role on CEs at the ecosystem level. Drivers themselves can indeed restructure the food web by changing the ecological community and through trophic cascading (Tomczak *et al.*, 2013; Heymans and Tomczak, 2016). This is due to the structuring power of some drivers on the ecosystem and may be one of the main processes leading to CEs at the ecosystem level of organization, as observed in Nogues *et al.* (2020) and Niiranen *et al.* (2013). This was visible on recycling under both CC cumu-
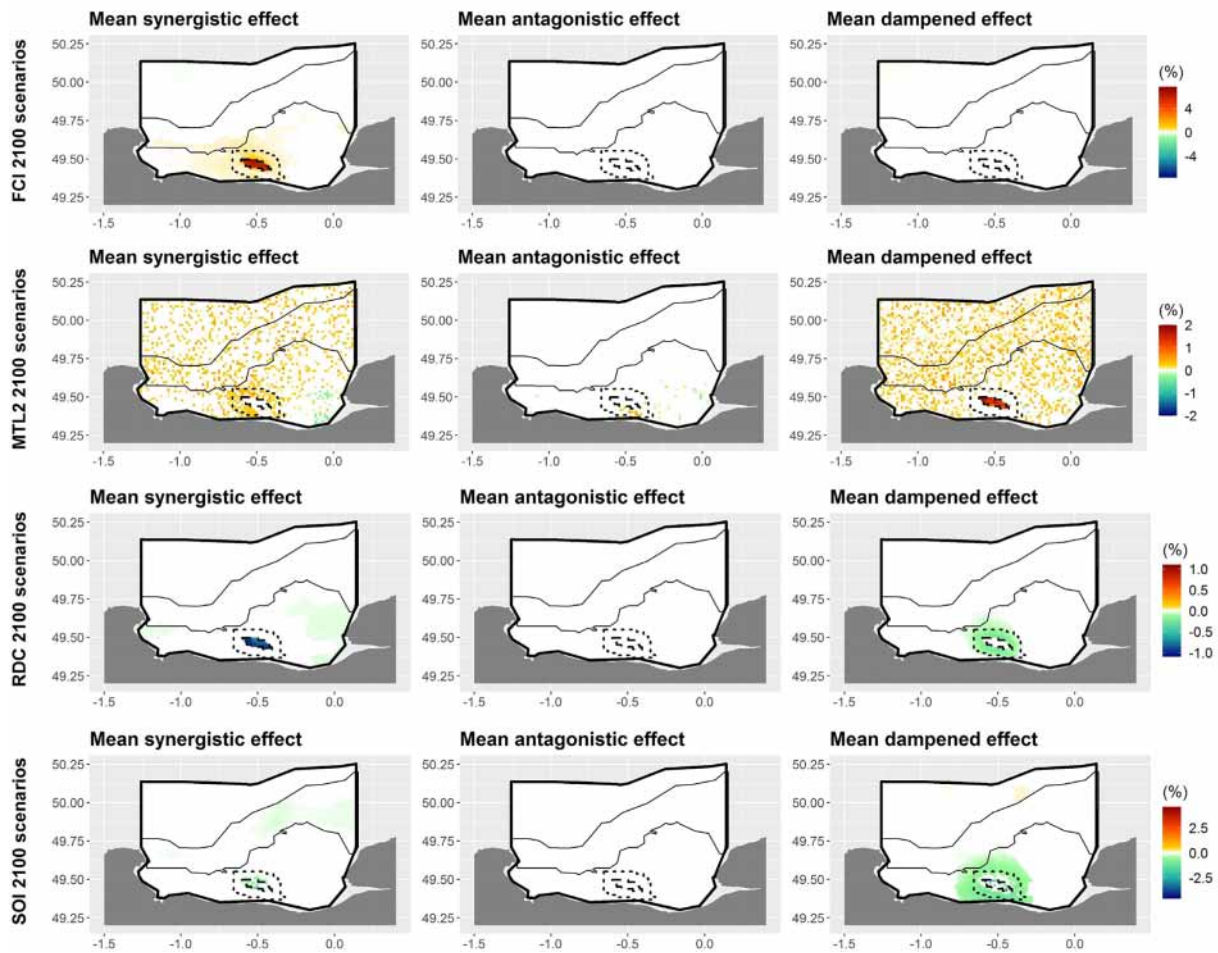
Figure 6. Strong CEs under the 2100 cumulative scenario according to the Cliff delta metric. The averaged CEs were mapped when the difference between the additive effect and the combined effect was considered large by the Cliff delta. Maps were sorted *per* row (ENA indices) and *per* column (cumulative effect). Warm colours, positive CEs relative to the reference model; cold colours, negative CEs relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.

lative scenarios. Taken separately, the OWF reduced system recycling, while CC increased it with varying intensities under the two 2050 and 2100 cumulative scenarios. When combined, CC and the OWF resulted in a synergistic increase of recycling under both cumulative scenarios (2050 and 2100). Therefore, the effect of the OWF may change under the influence of CC. CC is already known to restructure food webs (Montoya and Raffaelli, 2010; Walther, 2010) due to varying velocities of species drift (Van Der Putten *et al.*, 2010; Brose *et al.*, 2012). Such restructuring of the system can change energy distribution in the food web through trophic cascades (Carpenter *et al.*, 1985), and modify the effect of the OWF on recycling and lead to a positive synergistic effect. Ecosystems need to be monitored using holistic indices (Tomczak *et al.*, 2013) to detect potential ecosystem restructuring (Rilov *et al.*, 2020). Our results show that ignoring the plasticity of ecosystems to drivers and their effects on species relationships may hinder the detection of CEs on ecosystem functioning.

A driver effect on the ecosystem may also change over time, especially in the case of CC and its effect on species distribution (Martinez-Meyer, 2005). As the magnitude of the effect of CC on the ecosystem changed over time, the role of CC in the CE with the OWF changed too. This was visible through the different CEs of the two cumulative scenarios on

omnivory and flow redundancy. The effect was also distinguishable on the mean trophic level of the OWF region: While both cumulative scenarios displayed the same positive dampened effect on the mean trophic level, they are the result of different mechanisms. Under the 2050 cumulative scenario, the dampened positive effect resulted from the aggregation of fish by the OWF that mitigated the negative effect of CC on the mean trophic level (Supplementary materials 2 Figures S2–5); under the 2100 cumulative scenario, the effect of CC on the ecosystem structure limited the aggregating effect of the OWF on the mean trophic level (Supplementary materials 2 Figures S2–6 and S2–8). Thus, the dampened effect resulted from the aggregating effect of the OWF (Halouani *et al.*, 2020) under the 2050 scenario, while it resulted from the changed community structure across the entire eBoS under the 2100 scenario (Fulton, 2011; Pinsky *et al.*, 2013; Kleisner *et al.*, 2016). CC may indeed produce "winners" and "losers", and modify ecosystem structures up to a point where CE may change. Therefore, CEs should not be considered consistent over time because drivers like CC may change, so that continuous monitoring of ecosystems is required (Cocklin *et al.*, 1992; Spaling, 1994).

CC seems to have a preponderant role in the formation of CEs, especially under the 2100 scenario compared to the

2050 scenario, when the effect of CC becomes much stronger. For many ENA indices, the direction of CEs nearly always followed the direction of CC rather than the direction of the OWF. The only exceptions occurred under the 2050 cumulative scenario, when the effects of CC were weaker because ecosystem properties were less impacted by CC than in 2100 (Nogues *et al.*, 2022). This was visible for the negative dampened effect on the omnivory of the spillover region and for the positive dampened effect on the mean trophic level of the OWF region. This can be explained by the fact that CC under the 2050 scenario had limited or no effect compared to the effects of the OWF (Supplementary materials 2 Figures S2–5 and S2–13). In the other cases, CE acted in the same direction as CC did, with effects varying from synergistic to dampened along with limited antagonistic effects, despite the variability in fishing. Such results remain difficult to compare to meta-analyses of cumulative impacts (e.g. Hodgson and Halpern, 2019) because we used a new method to characterize combined effects. However, our results are in line with the idea that the cumulative responses to multiple drivers are often non-additive (Darling and Côté, 2008). Overall, the fact that CC appeared to be the predominant effect compared to the OWF, resulting in CEs closer to the effect of CC than to the effect of the OWF, further emphasized the need to consider the significant effects of CC in cumulative impact assessment and to better understand its potential structuring effects on species relationships (Wernberg *et al.*, 2012).

The increasing effect of CC on the ecosystem between the 2050 and the 2100 scenarios impacted the ecosystem's resilience. Under the 2050 scenario, the combined drivers tend to increase recycling, mean trophic level, omnivory, and relative redundancy of the flow, indicating a more resilient system to potential future disturbances. Higher SOI and relative flow redundancy could indeed be beneficial to the system's resilience, indicating an increased flexibility of the system. The complexity associated to the SOI has been linked to the system flexibility, which makes the ecosystem more resilient to disturbances (Fagan, 1997; Lobry *et al.*, 2008). Relative flow redundancy is also associated to ecological resilience because flow redundancy can act as a reserve to be used when the system is perturbed and makes it more resistant to disturbances (Ulanowicz *et al.*, 2009). Recycling can further improve ecosystem resilience, acting as a buffer to perturbation further indicating that the OWF could limit the effect of CC on the ecosystem's resilience in the spillover region (Saint-Béat *et al.*, 2015). The increased resilience of the system due to the OWF and its combined effect with CC is again in line with the idea that the habitat heterogeneity brought by the OWF can improve ecosystem resilience (Munguia *et al.*, 2011). However, with a strong effect of CC, this can only be true until CC restructures the system to a point where the OWF will potentially not have any effect on the ecosystem's resilience. Under the 2100 scenario, the lower SOI and the lower relative redundancy constitute signs of a lower ecological resilience compared to the 2050 scenario. The combined effect of the two drivers impairs the system's resilience under the 2100 scenario. This needs to be considered carefully as Ecospace—like Ecopath—does not take the potential adaptability of species into account, but follows trends of the relationship between CC and ecosystem resilience at different levels of organization (Harley *et al.*, 2006; Côté and Darling, 2010; Wernberg *et al.*, 2011).

Conclusion

Using ENA indices to study CEs on ecosystem functioning provides new insights into the functional pathways of cumulative responses. Such pathways seem inherently ecosystem-dependent, driver-dependent but more importantly effect-dependent. This is emphasized by the consequences of CC on species distribution: The location of the ecosystem and the differential sensitivity levels of the different species are unique to each case study. As such, the resulting structuring effect is specific to the community assemblage of the ecosystem. Thus, relations among drivers can be highly dependent on the studied system. This was previously theorized by Cocklin *et al.* (1992) and Spaling (1994) and shows that such studies should be encouraged all around the world to explore the wide variability of functional response to CEs (Gissi *et al.*, 2021). In the extended Bay of Seine, CEs resulting from the OWF and CC seem to change through time. While in 2050, CEs tend to benefit the ecosystem functioning, in 2100, with the increased impact of CC, CEs tend to negatively impact the ecosystem functioning. Studying the combine effects of multiple drivers on the functioning of ecosystems could allow us to better grasp the complexity of CEs and better guide ecosystem monitoring and management in the future.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability

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

Author contributions

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

Conflict of interest

The authors have no conflict of interest to declare.

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