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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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21 Abstract

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

36 **Key words:** coastal ecology, ecological network analysis, cumulative effects, ecosystem
37 functioning, resilience, combined drivers, climate change, offshore wind farm, fishing.

38 Highlights:

- 39 • Interactions between offshore wind farms and climate change can lead to a wide range
40 of cumulative effects on ecosystems regardless of fishing activities.
- 41 • The structuring role of climate change seems to have a predominant role in the
42 formation of cumulative effects.
- 43 • Cumulative effects appear heterogeneous across space, over time and among
44 ecosystem functional properties.
- 45 • In 2050, the combined effects of climate change and the wind farm remain positive for
46 ecological resilience.
- 47 • In 2100, interactions between climate change and the wind farm change, reducing
48 ecological resilience.

49 1 Introduction

50 When multiple anthropogenic drivers — fishing and climate change among others — co-
51 occur in an ecosystem, they often interact with each other to produce cumulative effects (CE)
52 on the ecosystems (Folt and Chen, 1999; Vinebrooke *et al.*, 2004). Cumulative effects have
53 been observed in many marine ecosystems (Crain *et al.*, 2008; Halpern and Fujita, 2013). They
54 can result in different ecosystem changes than the sum of the individual drivers, that can be
55 synergistic, antagonistic or dampened. These interactive effects occur at all the levels of
56 biological organization, from single organisms to complex and interconnected systems
57 (Stelzenmüller *et al.*, 2018). In ecosystems, CEs result from complex interactions among
58 ecosystem drivers and depend on ecosystem functioning (Breitburg *et al.*, 1998; Boyd and
59 Hutchins, 2012). They can emerge through interactions within the food web, via trophic
60 cascading. In a world subjected to intense human activities and climate change (IPCC, 2021),
61 understanding the effect of each individual driver is not enough. Interactions among drivers in
62 ecosystems must also be studied because they could represent a major threat for marine
63 conservation and management (Willstead *et al.*, 2017; Gissi *et al.*, 2021).

64 It is important to understand the full extent to which biotic and abiotic drivers affect
65 ecosystems to properly manage marine resources (Rombouts *et al.*, 2013; Heymans *et al.*,
66 2020), and where these effects take place (Halpern and Fujita, 2013). The European marine
67 spatial planning (MSP) directive (2014/89/EU) requests EU members to establish spatial
68 planning processes to achieve ecological, economic and social development. Ecosystem-based
69 management has been advocated as a key pillar for the sustainable management of marine
70 and coastal environments (Langlet and Rayfuse, 2018). As a result, CEs on the whole ecosystem
71 functioning must be considered across time and space to manage ecosystems efficiently. This
72 would ensure more accurate spatial zoning decisions and ecosystem-based management plans
73 (Buhl-Mortensen *et al.*, 2017; Le Tissier, 2020). Unfortunately, time passed until CEs were
74 properly considered in strategic environmental impact assessment (Bidstrup *et al.*, 2016), and
75 there is still an urgent need to further include them nowadays (Guşatu *et al.*, 2021).

76 Spatial cumulative assessment studies often fail to explore the complex nature of CEs
77 because (i) interactions among ecosystem components and drivers are frequently ignored, and
78 CEs are considered additive, and (ii) each driver is usually mapped using the expected footprint

79 of an impact, without considering the specific response of habitat / community types to the
80 tested drivers (Ban *et al.*, 2010; Halpern and Fujita, 2013; Kotta *et al.*, 2020; Guşatu *et al.*,
81 2021).

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

96 Ecological network analysis (ENA) indices can be used to link both ecosystem approaches
97 and cumulative assessment. ENA indices are utilized to understand the functioning of a food
98 web; they provide an integrative and holistic view of ecosystem functioning, organization and
99 structure (Ulanowicz, 1986; Baird and Ulanowicz, 1993; Borrett and Scharler, 2019). ENA
100 indices can be computed using food web modeling techniques and have been extensively
101 promoted as promising tools for ecosystem-based management (Ulrike *et al.*, 2018; Fath *et al.*,
102 2019; Safi *et al.*, 2019). They have already been used to study the CEs and the spatial effect of
103 multiple individual anthropogenic drivers (Nogues *et al.*, 2020; Nogues *et al.*, 2022).

104 Ecopath with Ecosim (EwE) is a food web modeling framework that can explore
105 cumulative impacts on ENA indices (Christensen and Walters, 2004). The spatialized version of
106 Ecopath – Ecospace – was used in Nogues *et al.* (2022) to compute maps of ENA indices in
107 order to understand the spatial organization and functioning of the extended Bay of Seine
108 ecosystem (eBoS, English Channel). Based on its functioning, the Bay of Seine was divided in
109 multiple five functional regions (Nogues *et al.*, 2022). These five regions were used to

110 characterize the potential individual effects of multiple drivers using ENA indices. These drivers
111 included the potential effects of climate change (CC) on species distribution and the
112 exploitation of the offshore wind farm (OWF) of Courseulles-sur-Mer (in the Bay of Seine)
113 under varying fishing effort.

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

120 2 Materials and methods

121 2.1 Study area

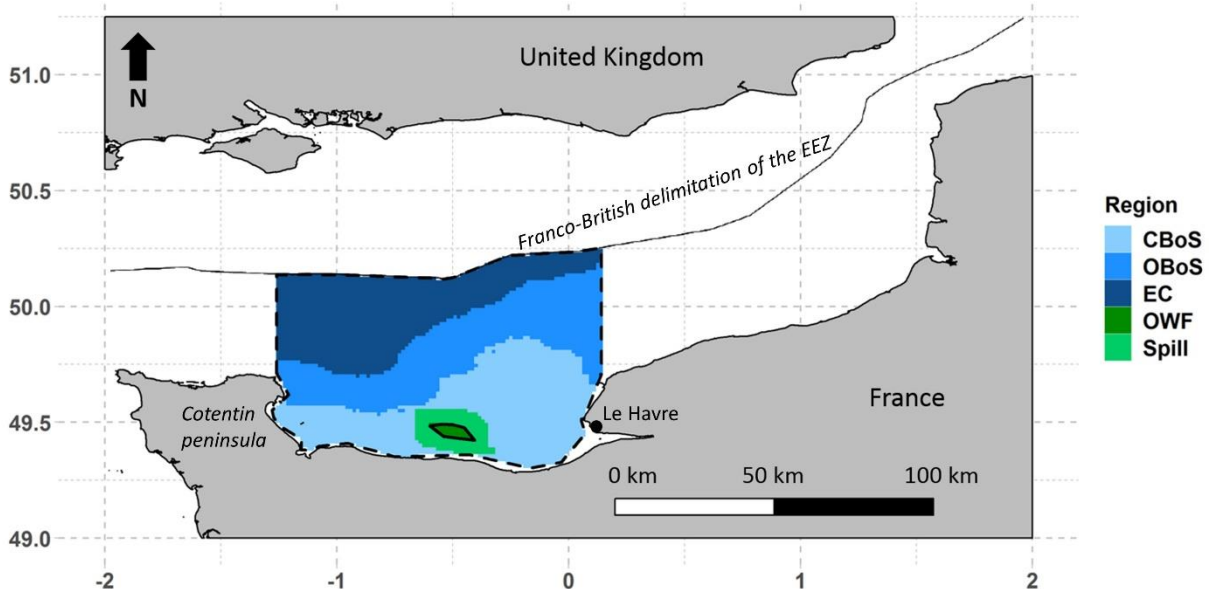
122 The extended Bay of Seine (eBoS) Ecospace model covers the coastal ecosystem of the
123 Bay of Seine, from the Cotentin peninsula to Le Havre and from the French coastline to the
124 French-British delimitation of the Exclusive Economic Zones (Figure - 1). It is a shallow coastal
125 ecosystem open onto the English Channel in the north, with depth varying from 5 m to 70 m
126 in the paleo-valley of the Seine (mean 35 m). It covers 13,500 km² and is mainly composed of
127 gravel, coarse sand in the offshore part of the bay, while fine sand and muddy fine sand are
128 located near the coast (Dauvin, 2015). This area is heavily anthropized and is home to many
129 human activities including fishing, aggregate extraction, marine renewable energy, tourism,
130 fret transport, and pleasure sailing among others (Dauvin, 2019).

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

140 functional region and named them “Offshore wind farm” (OWF) and “Spillover region” (Spill).

141 All the regions were mutually exclusive (Figure - 1).

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144 **Figure - 1 Map of the eastern part of the English Channel and location of**
145 **the eBoS Ecospace model.**

146 The Ecospace model was divided into five regions: CBoS (Coastal Bay of
147 Seine), OBoS (Offshore Bay of Seine), and EC (Central English Channel); OWF
148 (Offshore wind farm) and Spill (Spillover region surrounding the OWF). All
149 regions are exclusive.

150 2.2 Ecospace spatialized food web modeling

151 The eBoS food web was modeled with a modified version of Ecopath with Ecosim (EwE
152 6) software (Pauly *et al.*, 2000). This software can be used to model marine food webs: in a
153 static way with Ecopath (Pauly *et al.*, 2000), in a time-dynamic way with Ecosim (Christensen
154 and Walters, 2004), and temporal-spatial way with Ecospace (Walters *et al.*, 1999; Christensen
155 *et al.*, 2014). The EwE 6 version we used was specially modified to compute food web indices
156 (Nogues *et al.*, 2022). Following Nogues *et al.* (2022), this study is based on Halouani *et al.*
157 (2020) to model the eBoS ecosystem (**Figure - 2.A**).

158 The original eBoS Ecopath was composed of 42 groups, including 40 living groups with a
159 wide variety of marine species – from phytoplankton and bacteria to bottlenose dolphins and
160 sea birds – and two non-living groups; Detritus and Discards (Supplementary materials 1 Table

161 S1 - 1). This Ecopath model served as a basis to build an Ecosim time-dynamic model using 21
162 time series of catches (Système d'Information Halieutique, 2017) and eight time series of
163 biomass from multiple stock assessment surveys (2000 to 2015) (Halouani *et al.*, 2020). An
164 Ecospace model was later built to spatially model the eBoS ecosystem. The eBoS model map
165 was composed of 4,907 cells with a resolution of 0.015° x 0.015°, and each cell modeled a time-
166 dynamic Ecosim food web. Species distributions inside the eBoS Ecospace model were driven
167 using a depth map from the General Bathymetric Chart of the Oceans (GEBCO:
168 <https://www.gebco.net/>), a primary production map from SeaWiifs representing the relative
169 chlorophyll *a* concentration in the bay in 2000 (<https://podaac.jpl.nasa.gov/>) and multiple
170 environmental driver maps for 27 of the 40 trophic groups (Supplementary materials 1 Table
171 S1 – 1 to S1 - 3; Figure S1 – 2 to S1 – 36; Bourdaud *et al.*, 2021; Halouani *et al.*, 2020; Nogues
172 *et al.*, 2022). Environmental driver maps were built from suitability index maps computed from
173 niche models by Ben Rais Lasram *et al.* (2020), and were used to define habitat suitability for
174 the specified species (Christensen *et al.*, 2014). Suitability index maps were computed using
175 2005 – 2012 climate and habitat parameters (temperature, salinity, type of substrate, depth,
176 seafloor slope, and orientation to the north). All the parameters of the eBoS model are
177 available in Halouani *et al.* (2020), Bourdaud *et al.* (2021), and Nogues *et al.* (2022).

178 2.3 Modeling of anthropogenic drivers: effects of climate change the offshore wind
179 farm of Courseulles-sur-Mer and fishing.

180 We focused on two main anthropogenic drivers in the eBoS Ecospace model (Nogues *et*
181 *al.*, 2022): climate change and the operation of an offshore wind farm.

182 To model the effects of CC, the spatio-temporal framework of *EwE* (Steenbeek *et al.*,
183 2013) was used. This Ecospace tool can modify Ecospace inputs over time, such as
184 environmental driver maps. In the present study, it was used to replace the initial suitability
185 index maps computed from 2005 - 2012 climate parameters of the baseline eBoS Ecospace
186 model, with new suitability index maps simulating the effects of CC on species distribution
187 (Nogues *et al.*, 2022). Two conditions were tested — using two new sets of suitability index
188 maps computed at two different horizons (2050 and 2100) — of the IPCC “Business as usual”
189 climate change projection (RCP 8.5, considered the most likely scenario; Schwalm *et al.*, 2020).
190 One condition represented the 2050 decade (2041 – 2050), while another represented the
191 2100 decade (2091 – 2100) (Nogues *et al.*, 2022, **Figure - 2**). By replacing the reference

192 “current” suitability index maps of the baseline eBoS model during the Ecospace model run,
193 with either the 2050 or the 2100 condition suitability index maps, we changed the habitat
194 suitability for the eBoS trophic groups according to the effect of CC on their suitability. After
195 replacing the suitability index for each CC condition (2050 and 2100), the Ecospace model was
196 run to equilibrium. In doing so, CC-induced changes to the environmental parameters which
197 affected the habitat suitability of the impacted groups in Ecospace. Following the foraging
198 arena theory (Walters *et al.*, 1997, 1999), changes in habitat suitability affect consumption by
199 the groups in the cells and modify their production and biomass and thus their distribution and
200 dynamic (Christensen *et al.*, 2014).

201 The long-lasting effects of the future offshore wind farm of Courseulles-sur-Mer were
202 modeled following previous works including Halouani *et al.* (2020) who first modeled the
203 reserve effect of the OWF. We improved on Halouani *et al.* (2020): by modeling a limited
204 closure of the farm following the owners’ proposal to “optimize” fishing inside the farm (~15
205 %, Raoux *et al.*, 2018, 2019) and by modeling the potential reef effect of the OWF (Nogues *et al.*
206 *et al.*, 2022). The reef effect was simulated based on Raoux *et al.* (2017), which used Ecosim to
207 simulate the introduction of new hard substrates to the Courseulles-sur-Mer ecosystem
208 (**Figure - 2.A**). Using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013), biomass
209 changes observed in Raoux *et al.* (2017) due to the reef effect were transposed to new
210 environmental driver maps to increase the habitat suitability of multiple benthic and demersal
211 groups inside the OWF (Table - 1 and supplementary materials 1 Table S1 – 4; Nogues *et al.*,
212 2022). Combined with the 15% closure to fishing, this means that this study focuses on both
213 the reef and the reserve effects of the OWF, two effects considered as highly structuring on
214 the ecosystems (Langhamer, 2012; De Mesel *et al.*, 2015).

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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).

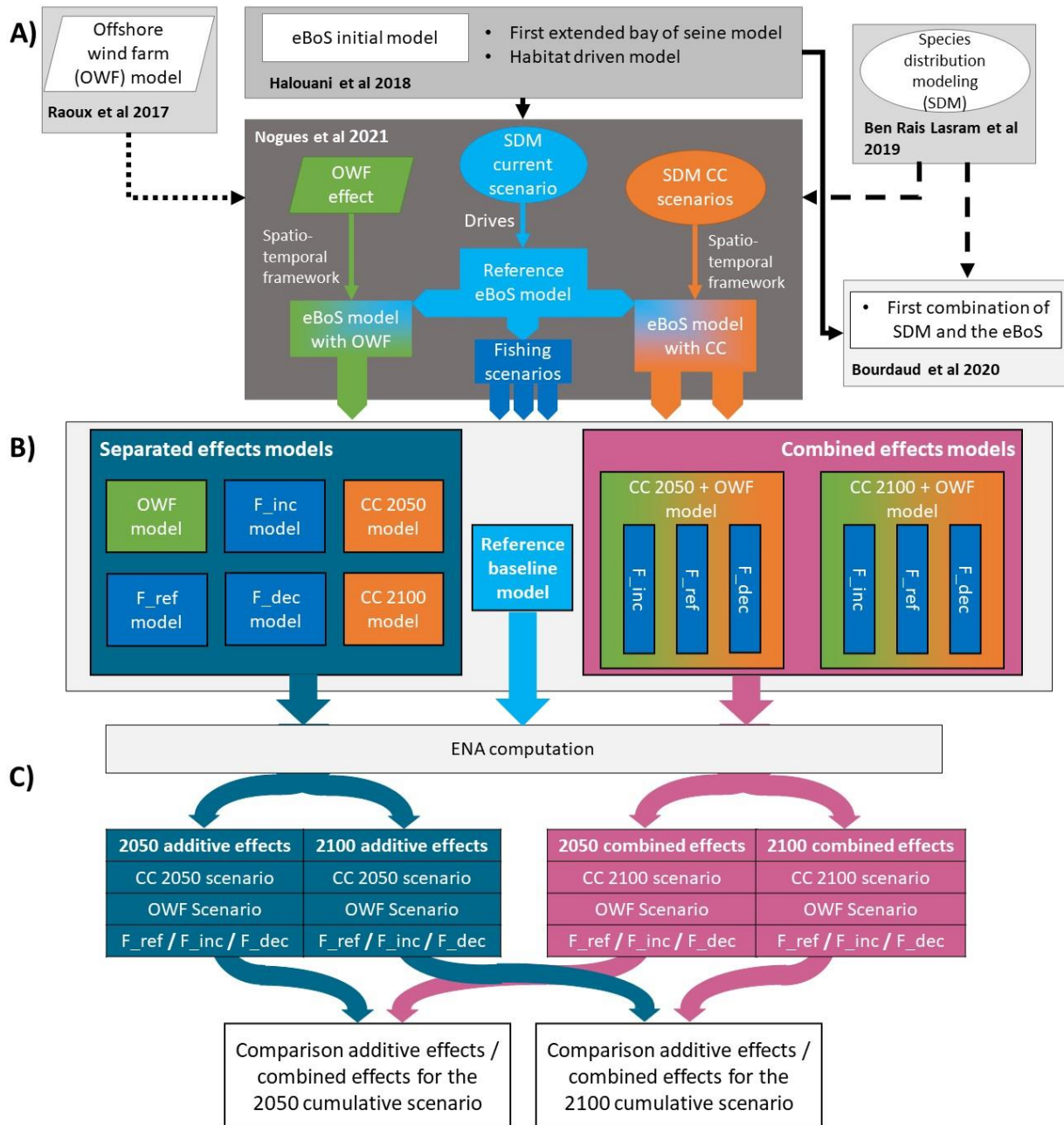
OWF presence	eBoS groups	Ecospace reef environmental driver
No	All	1.00
Yes	Surface feeders seabirds	6.11
	Fish Atlantic cod	3.49
	Fish whiting	4.18
	Fish pouting	2.32
	Fish benthos feeders	2.07
	Fish sole	1.93
	Fish flounder	4.37
	Fish dab	4.37
	Benthic inv. Predators	1.02
	Benthic inv. filter feeders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

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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 Table 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 Figure 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:

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- 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).



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236 **Figure - 2 Diagram of the modeling framework. Describes vertically: A)**
 237 **previous work leading up to this study and their relationships (solid: same**
 238 **model; dashed: same approach; dotted: used data), B) the modeling**
 239 **framework used in this study, C) the cumulative effects assessment**
 240 **procedure.**

241 2.4 Ecological network analysis

242 The scenarios built in Nogues *et al.* (2022) were used to compute maps of ENA indices
 243 using the “EnaR” Ecospace plugin (Nogues *et al.*, 2022). This plugin available in a modified
 244 version of *Ewe* 6 is used to create Scientific Committee for Ocean Research (SCOR) formatted
 245 files for each cell of the Ecospace model at each time step. SCOR files contain all the data

246 needed to create maps of ENA indices using the R package “EnaR” (Borrett and Lau, 2014).
 247 Each cell of the Ecospace model had ENA values that were used to build ENA maps using the
 248 same resolution as Ecospace (Supplementary materials 1 Figure S1 - 1). We selected four ENA
 249 indices to describe and understand the functioning and organization of the food web (Table -
 250 2), based on previous lists of ENA indices considered promising for ecosystem management
 251 due to their insights into ecosystem functioning and ecosystem resilience (Fath *et al.*, 2019;
 252 Safi *et al.*, 2019). Each cumulative scenario had three sets of ENA results – one *per* fishing
 253 scenario.

254 **Table - 2 ENA indices computed with EnaR from Ecospace SCOR files (see**
 255 **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; Christensen, 1995)
System omnivory (SOI)	Determine the level of omnivory of the system, <i>i.e.</i> , 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)

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257 2.5 Assessment of cumulative effects

258 ENA indices can assess the cumulative effects on the ecosystem properties, as described
 259 in Nogues *et al.* (2020). The methodology of Travers-Trolet *et al.* (2014) and Fu *et al.* (2018)
 260 was applied to determine the type of CE. This method considers that CEs can be synergistic,
 261 antagonistic or dampened. It also considers the direction of the effect on the studied index
 262 (positive or negative relative to the reference).

263 To determine CEs, we computed the relative index change (delta) between the reference
 264 scenario and each independent driver (eq. 1, e.g., the OWF alone or one of the CC conditions
 265 (2050 or 2100) or one of the fishing scenarios) for all ENA indices.

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

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

268 Then, we summed the ΔI_s^{sep} of each driver (CC, OWF and fishing) for each combination
 269 (F_red, F_inc, F_ref) in each cumulative scenario (cumulative 2050 and cumulative 2100,
 270 **Figure** - 2.B and C). This yielded three additive effects $\sum \Delta I_s^{sep}$ per cumulative scenario
 271 ($\sum \Delta I_s^{sep} F_{red}$, the $\sum \Delta I_s^{sep} F_{inc}$ and the $\sum \Delta I_s^{sep} F_{ref}$). To characterize CEs, we compared the
 272 three additive effects ($\sum \Delta I_s^{sep} F_{red}$ & $\sum \Delta I_s^{sep} F_{inc}$ & $\sum \Delta I_s^{sep} F_{ref}$) to the three
 273 corresponding combined effects ($\Delta I_c^{cum} F_{red}$ & $\Delta I_c^{cum} F_{inc}$ & $\Delta I_c^{cum} F_{ref}$), (Figure - 3, eq. 2)
 274 for the 2050 and 2100 cumulative scenarios.

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

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

277 2.6 Comparison of additive effects and combined effects

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



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Figure - 3 Comparison of the additive and combined effects of drivers to determine the resulting cumulative effect of drivers on ENA indices.

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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; case 7: negative antagonistic.

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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 (4,907 comparisons). It was chosen because it is a non-parametric effect size metric that can be used to compare datasets with 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) ($|\partial \text{Cliff}| < 0.474$), 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.

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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 climate change 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

309 increase to 0.3, a 500% increase compare to the reference. If, on the other hand, driver A's
310 response is increased simultaneously to 0.8, then the habitat capacity will increase to 0.48.
311 While this will still result in a 500% increase of the habitat capacity, the absolute increase of
312 the habitat capacity will be different due to driver A (a 0.25 increase in the first case, and a 0.4
313 increase in the second case). Compared to the reference, the combine effect of drive A and B
314 will thus have a higher absolute effect than each effect taken separately. This difference in the
315 absolute effect of the drivers on the habitat suitability is akin to a cumulative response, where
316 the intensity of one driver may impact the intensity of another. In this case, however, this is
317 governed by the Ecospace equations. To determine what are the consequences of the habitat
318 suitability model on CEs, the same cumulative assessment method was used to distinguish CEs
319 on the habitat suitability and on the biomass of the different groups. This assessment was
320 made by combining the effect of climate change in both conditions (2050 and 2100) and the
321 reef effect of the OWF.

322 3 Results

323 3.1 Cumulative effects in the eBoS regions

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

330 The average additive effect was an outlier to the average combined effect for the
331 recycling index (FCI), the mean trophic level (MTL2) and relative flow redundancy (RDC),
332 despite variability (i) inside the OWF sub-region and (ii) among the three fishing scenarios
333 within each cumulative scenario (Figure - 4). Under the 2050 cumulative scenario, CEs inside
334 the OWF were always positive – positive synergistic for the FCI and positive dampened for the
335 MTL2 and RDC. Under the 2100 cumulative scenario, CEs within the OWF were similar to those
336 under the 2050 cumulative scenario for FCI and MTL 2 – positive synergistic for the FCI and
337 dampened positive for the MTL2 (Figure - 4). However, a negative CE – negative synergistic for
338 relative redundancy (RDC, Figure - 4) – was found under the 2100 cumulative scenario that was

339 not found under the 2050 cumulative scenario. Another region that seemed to exhibit a CE
 340 was the Spillover region under the 2050 cumulative scenario, for the system omnivory (SOI).
 341 However, this effect was not as clear-cut as in the OWF region because there was greater
 342 variability within the region.

343 **Table - 3 Comparison between the cumulative effects (CE) visible on the**
 344 **habitat capacity and on the biomass of the groups in 2050 and 2100.**

345 Red color indicates the degree of difference between CE (different CE with
 346 same direction < opposite CE direction). Abbreviations include: positive
 347 (pos.), negative (neg.) and invertebrate (inv.).

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.

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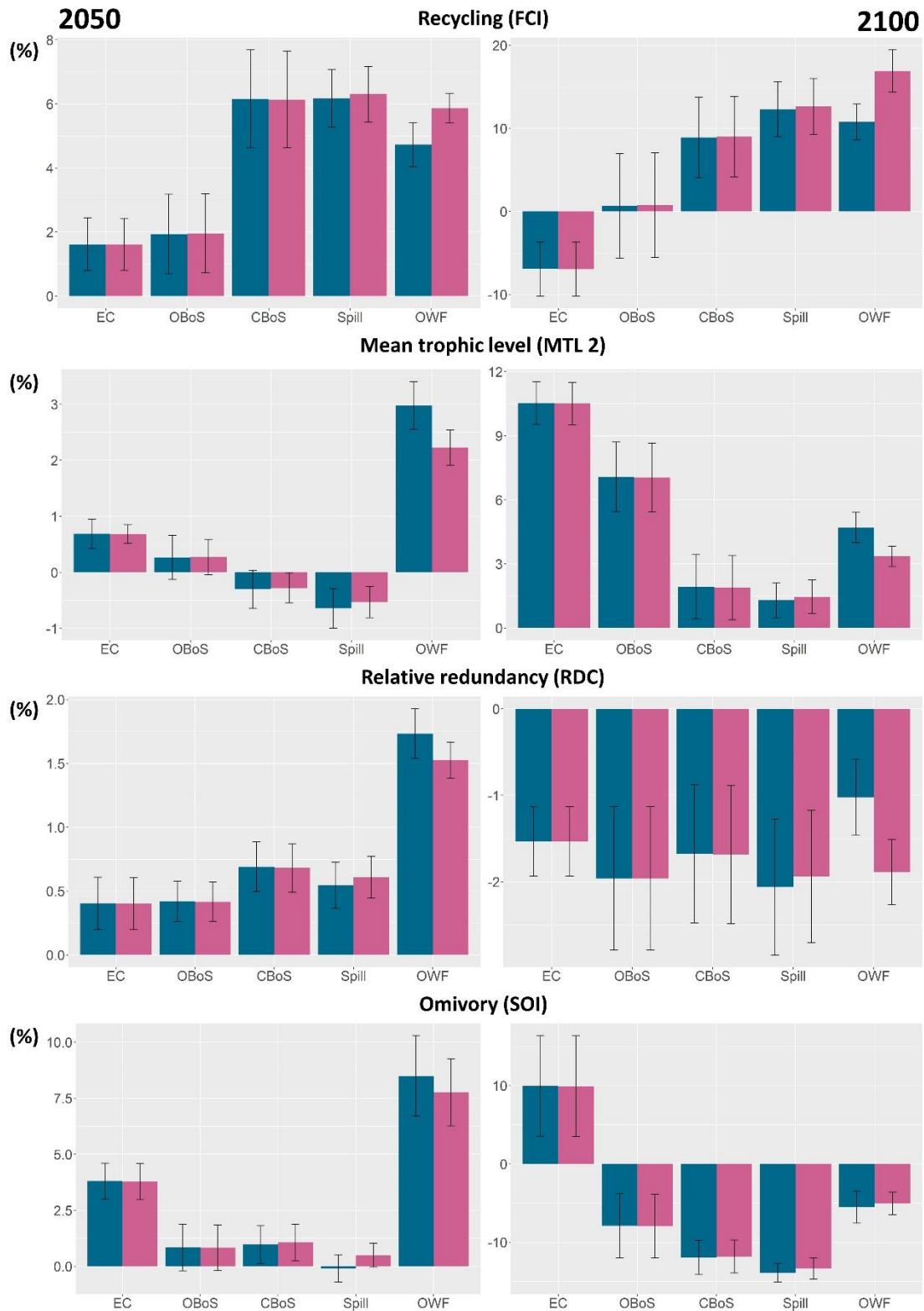


Figure - 4 Regional differences in percent between the averaged additive effect (blue) and the averaged combined effect (red) under the two cumulative scenarios (2050 left column and 2100 right column). Regions

355 **include: English Channel (EC); Offshore Bay of Seine (OBoS); Coastal Bay of**
356 **Seine (CBoS); Spillover (Spill); Offshore wind farm (OWF).**

357 The standard deviation for the cumulative scenario was calculated with the
358 values of all the cells of the given region, for all the combinations of drivers
359 (F_ref, F_inc and F_red), and was pictured with error bars. Error bars show
360 the standard deviations within the regions and among the driver
361 combinations under each cumulative scenario.

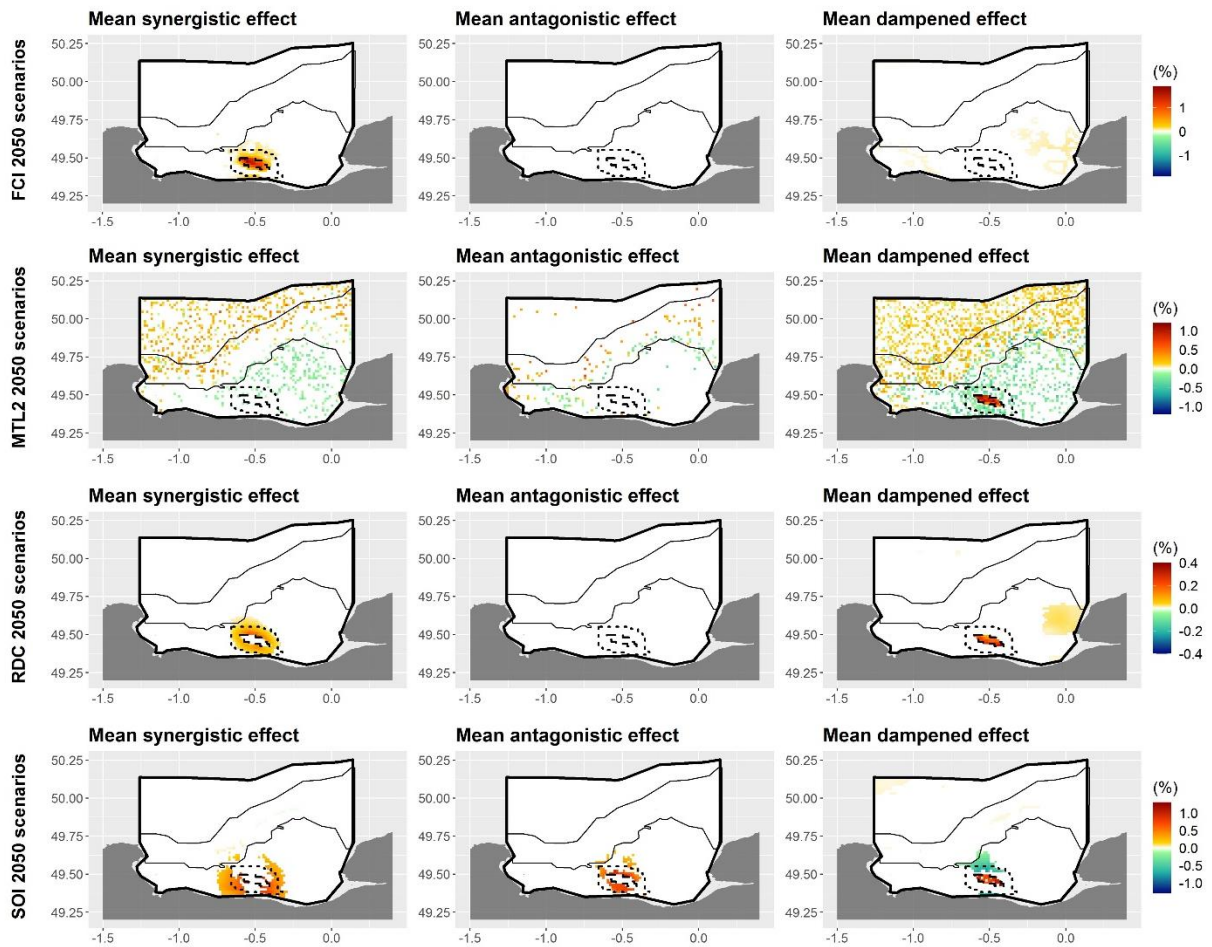
362 3.2 Spatial cumulative effects

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

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

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

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Figure - 5 Strong cumulative effects under the 2050 cumulative scenario according to the Cliff delta metric.

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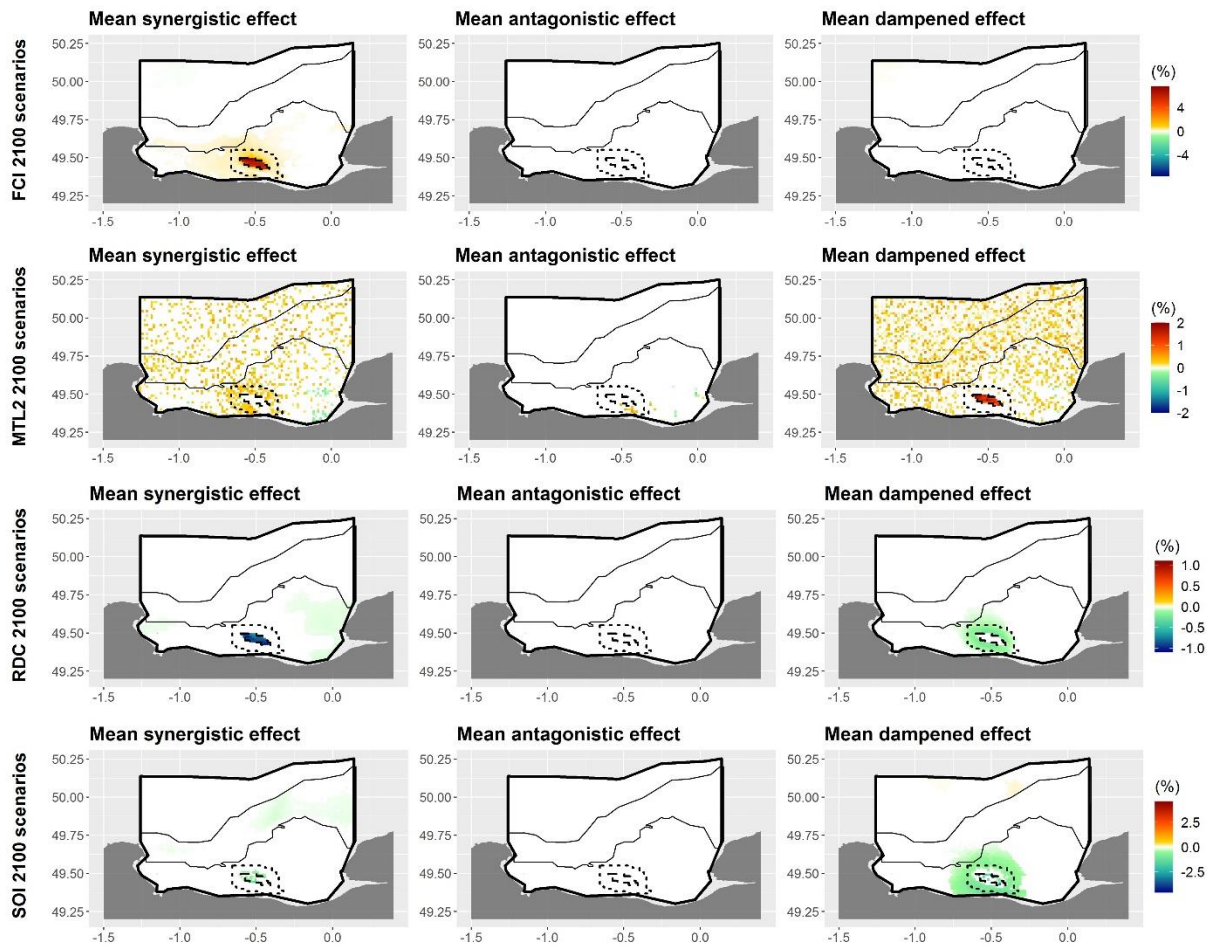
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The averaged cumulative effects were mapped when the difference between the additive effect and the combined effect was considered large by the Cliff delta. Maps were sorted *per row* (ENA indices) and *per column* (cumulative effect). Warm colors, positive cumulative effects relative to the reference model; cold colors, negative cumulative effects relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.



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Figure - 6 Strong cumulative effects under the 2100 cumulative scenario according to the Cliff delta metric.

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The averaged cumulative effects 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 colors, positive cumulative effects relative to the reference model; cold colors, negative cumulative effects relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.

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4 Discussion

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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. 2021). 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

413 (Ainsworth *et al.*, 2011). Unfortunately, our fishing scenarios did not enable us to do so directly,
414 but rather through the consideration of fishing variability.

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

427 4.1 Mapping of cumulative effects using ecosystem approaches

428 Cumulative effects mainly occurred within the OWF region, were both anthropogenic
429 drivers – CC and the OWF – coincide. This was mainly visible inside the OWF region, where the
430 differences between the habitat capacity of the separate and combined effects were observed.
431 However, CE were not only visible on the species impacted by both drivers, but on the
432 functioning and structure of the entire ecosystem. Multiple ecosystem indices showed this,
433 including the recycling (FCI), the mean trophic level of the consumers (MTL 2) and the relative
434 redundancy of the flows (RDC). This further confirmed the importance of considering larger-
435 scale drivers like climate change when assessing the environmental impact of local strategic
436 activities (Willstead *et al.*, 2017). Indeed, local and global drivers may interact with each other
437 through trophic cascading, leading to unsuspected consequences on the ecosystem at the local
438 scale (Brown *et al.*, 2013). Even at the trophic group scale, when the habitat capacity model
439 predicted one type of cumulative response, the CE visible on the biomass of the group was
440 different due to trophic relationships with other groups. This highlights the importance of
441 considering the combined effects of local and global drivers on complex systems such as food
442 webs (Boyd and Hutchins, 2012; Nogues *et al.*, 2021), whether in space or in the system itself.

443 Cumulative effects were important across the OWF region, but it was not the only region
444 with noticeable effects. They were also visible in multiple cells outside the OWF region –
445 regions that did not display CE on the habitat capacity – such as in the spillover region
446 surrounding the farm and the coastal region. Moreover, the extent of these effects differed
447 among ENA indices, with heterogeneous CEs inside and outside the OWF region. The varying
448 CEs *per* ENA index, already observed by Nogues *et al.* (2020), indicated that CEs can differ
449 depending on the ecosystem property, and that CEs result from different trophic relationships
450 which can be related to multiple cumulative pathways (Spaling, 1994). A cumulative impact
451 may affect differently each species of an ecosystem (Fu *et al.*, 2018; Ortega-Cisneros *et al.*,
452 2018), and the same goes for ecosystem properties (*e.g.*, recycling, omnivory or flow
453 redundancy). For example, CEs on flow redundancy may be linked to simultaneous changes at
454 multiple trophic levels, which can result in a different CE on the system omnivory. As habitat
455 and ecological communities are not homogeneous in space and ecological responses to drivers
456 differ among trophic groups (Schiel *et al.*, 2014; Epstein and Smale, 2018), such coordination
457 may vary across space. Moreover, trophic groups may not move at the same rate in the
458 ecosystem. Therefore, ecosystem responses to multiple drivers should not be generalized: two
459 given drivers may interact differently in different ecosystems (Cocklin *et al.*, 1992; Gissi *et al.*,
460 2021), and may not interact uniformly within a given ecosystem. Current cumulative
461 assessment works often overlook such variability (Ban *et al.*, 2010; Halpern and Fujita, 2013;
462 Kotta *et al.*, 2020). Therefore, ecosystem approaches should be promoted to model these
463 structures and properly assess the multiple effects of combined drivers on the ecosystem. This
464 could also greatly help the mapping of the potential interactions between two large-scale
465 drivers like fishing and CC because they may have complex spatial patterns of CEs depending
466 on ecosystem heterogeneity that conventional CE assessment may not be able to grasp.

467 4.2 Cumulative effects and climate change

468 Ecosystem approaches also benefit from their ability to detect potential ecosystem
469 restructuring, which plays a key role on CEs at the ecosystem level. Drivers themselves can
470 indeed restructure the food web by changing the ecological community and through trophic
471 cascading (Tomczak *et al.*, 2013; Heymans and Tomczak, 2016). This is due to the structuring
472 power of some drivers on the ecosystem and may be one of the main processes leading to CEs
473 at the ecosystem level of organization, as observed in Nogues *et al.* (2020) and Niiranen *et al.*

474 (2013). This was visible on recycling under both CC cumulative scenarios. Taken separately, the
475 OWF reduced system recycling, while CC increased it with varying intensities under the two
476 2050 and 2100 cumulative scenarios. When combined, CC and the OWF resulted in a
477 synergistic increase of recycling under both cumulative scenarios (2050 and 2100). Therefore,
478 the effect of the OWF may change under the influence of CC. CC is already known to
479 restructure food webs (Montoya and Raffaelli, 2010; Walther, 2010) due to varying velocities
480 of species drift (Van Der Putten *et al.*, 2010; Brose *et al.*, 2012). Such restructuring of the
481 system can change energy distribution in the food web through trophic cascades (Carpenter
482 *et al.*, 1985), and modify the effect of the OWF on recycling and lead to a positive synergistic
483 effect. Ecosystems need to be monitored using holistic indices (Tomczak *et al.*, 2013) to detect
484 potential ecosystem restructuring (Rilov *et al.*, 2020). Our results show that ignoring the
485 plasticity of ecosystems to drivers and their effects on species relationships may hinder the
486 detection of CEs on ecosystem functioning.

487 A driver effect on the ecosystem may also change over time, especially in the case of CC
488 and its effect on species distribution (Martinez-Meyer, 2005). As the magnitude of the effect
489 of CC on the ecosystem changed over time, the role of CC in the CE with the OWF changed too.
490 This was visible through the different CEs of the two cumulative scenarios on omnivory and
491 flow redundancy. The effect was also distinguishable on the mean trophic level of the OWF
492 region: while both cumulative scenarios displayed the same positive dampened effect on the
493 mean trophic level, they are the result of different mechanisms. Under the 2050 cumulative
494 scenario, the dampened positive effect resulted from the aggregation of fish by the OWF that
495 mitigated the negative effect of CC on the mean trophic level (Supplementary materials 2
496 Figure S2 - 5); under the 2100 cumulative scenario, the effect of CC on the ecosystem structure
497 limited the aggregating effect of the OWF on the mean trophic level (Supplementary materials
498 2 Figure S2 – 6 & Figure S2 - 8). Thus, the dampened effect resulted from the aggregating effect
499 of the OWF (Halouani *et al.*, 2020) under the 2050 scenario, while it resulted from the changed
500 community structure across the entire eBoS under the 2100 scenario (Fulton, 2011; Pinsky *et al.*,
501 2013; Kleisner *et al.*, 2016). Climate change may indeed produce “winners” and “losers”,
502 and modify ecosystem structures up to a point where CE may change. Therefore, CEs should
503 not be considered consistent over time because drivers like CC may change, so that continuous
504 monitoring of ecosystems is required (Cocklin *et al.*, 1992; Spaling, 1994).

505 CC seems to have a preponderant role in the formation of CEs, especially under the 2100
506 scenario compared to the 2050 scenario, when the effect of CC becomes much stronger. For
507 many ENA indices, the direction of CEs nearly always followed the direction of CC rather than
508 the direction of the OWF. The only exceptions occurred under the 2050 cumulative scenario,
509 when the effects of CC were weaker because ecosystem properties were less impacted by CC
510 than in 2100 (Nogues *et al.*, 2022). This was visible for the negative dampened effect on the
511 omnivory of the spillover region and for the positive dampened effect on the mean trophic
512 level of the OWF region. This can be explained by the fact that CC under the 2050 scenario had
513 limited or no effect compared to the effects of the OWF (Supplementary materials 2 Figure S2
514 – 5 & S2 - 13). In the other cases, CE acted in the same direction as CC did, with effects varying
515 from synergistic to dampened along with limited antagonistic effects, despite the variability in
516 fishing. Such results remain difficult to compare to meta-analyses of cumulative impacts (*e.g.*,
517 Hodgson and Halpern, 2019) because we used a new method to characterize combined effects.
518 However, our results are in line with the idea that the cumulative responses to multiple drivers
519 are often non-additive (Darling and Côté, 2008). Overall, the fact that CC appeared to be the
520 predominant effect compared to the OWF, resulting in CEs closer to the effect of CC than to
521 the effect of the OWF, further emphasized the need to consider the significant effects of CC in
522 cumulative impact assessment and to better understand its potential structuring effects on
523 species relationships (Wernberg *et al.*, 2012).

524 The increasing effect of CC on the ecosystem between the 2050 and the 2100 scenarios
525 impacted the ecosystem's resilience. Under the 2050 scenario, the combined drivers tend to
526 increase recycling, mean trophic level, omnivory and relative redundancy of the flow,
527 indicating a more resilient system to potential future disturbances. Higher system omnivory
528 and relative flow redundancy could indeed be beneficial to the system's resilience, indicating
529 an increased flexibility of the system. The complexity associated to the system omnivory has
530 been linked to the system flexibility, which makes the ecosystem more resilient to disturbances
531 (Fagan, 1997; Lobry *et al.*, 2008). Relative flow redundancy is also associated to ecological
532 resilience because flow redundancy can act as a reserve to be used when the system is
533 perturbed, and makes it more resistant to disturbances (Ulanowicz *et al.*, 2009). Recycling can
534 further improve ecosystem resilience, acting as a buffer to perturbation further indicating that
535 the OWF could limit the effect of CC on the ecosystem's resilience in the spillover region (Saint-

536 B  at *et al.*, 2015). The increased resilience of the system due to the OWF and its combined
537 effect with CC is again in line with the idea that the habitat heterogeneity brought by the OWF
538 can improve ecosystem resilience (Munguia *et al.*, 2011). However, with a strong effect of CC,
539 this can only be true until CC restructures the system to a point where the OWF will potentially
540 not have any effect on the ecosystem's resilience. Under the 2100 scenario, the lower system
541 omnivory and the lower relative redundancy constitute signs of a lower ecological resilience
542 compared to the 2050 scenario. The combined effect of the two drivers impairs the system's
543 resilience under the 2100 scenario. This needs to be considered carefully as Ecospace – like
544 Ecopath – does not take the potential adaptability of species into account, but follows trends
545 of the relationship between CC and ecosystem resilience at different levels of organization
546 (Harley *et al.*, 2006; C  t   and Darling, 2010; Wernberg *et al.*, 2011).

547 Conclusion

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

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Data availability statement

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

Author contribution

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

Competing interest statement

The authors have no conflict of interest to declare.

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