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

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## 35 Abstract

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

50 **Key words:** Ecological network analysis, ENA, Ecospace, trophic structure, ecosystem  
51 functioning, climate change, Offshore wind farm, fishing effects, species distribution.

### 52 Highlights:

- 53 • Ecological network analysis describes the spatial effects of multiple environmental  
54 drivers on the functioning of the extended Bay of Seine ecosystem.
- 55 • Climate change effect on species distribution had strong structuring effects on the  
56 ecosystem.
- 57 • Two fishing scenarios linked to Brexit (increased and decreased fishing) were tested;  
58 they had limited effects on ecosystem functioning compared to the effects of climate  
59 change on species distribution.
- 60 • Ecological network analysis distinguished vulnerable areas that might require special  
61 attention in terms of ecological management.

62

## 63 1 Introduction

64 Marine ecosystems are crucial for human societies because they provide many services  
65 such as food provisioning, nutrient regulation, habitat maintenance and climate mitigation  
66 (Peterson and Lubchenco, 1997). Marine ecosystems are subject to pressures from human  
67 activities (Halpern *et al.*, 2008) and their subsequent detrimental impacts. Anthropogenic  
68 pressure is predicted to keep on increasing in the next decades due to the growing human  
69 needs (MEA *et al.*, 2005). This is reflected in the expanding number of offshore wind farms  
70 (OWFs) to meet the need for greener energy. The environmental impacts of OWFs occur in  
71 three phases: i) during the construction phase impacts may be considered temporary, the  
72 same can be said of the ii) decommission phase while iii) during the operational phase impacts  
73 are longer lasting (Petersen and Malm, 2006). The most significant long-lasting impacts of the  
74 operational phase on the whole ecosystem functioning include the reef effect caused by the  
75 turbine structures and the reserve effect resulting from fishing closure (Raoux *et al.*, 2019;  
76 Degraer *et al.*, 2020). Direct anthropogenic activities are not the only driver of ecosystems:  
77 climate change (CC) may also have many hard to predict effects (Hoegh-Guldberg and Bruno,  
78 2010; Poloczanska *et al.*, 2016; Winder and Sommer, 2012a). These effects include (among  
79 others) drifts in species distribution (Cheung *et al.*, 2009) and changing physiological rates  
80 (Brierley and Kingsford, 2009). Ecosystems are complex and interconnected. Unpredictable  
81 effects on several of their components could cascade through trophic chains and interactions,  
82 limit their resilience and thus facilitate regime shifts and ecosystem collapses (Levin and  
83 Lubchenco, 2008). In this situation, there is a growing need for integrative approaches to  
84 understand the sensitivity of such ecosystems to a wide variety of drivers.

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

93 Ecological network analysis (ENA) is promising because it is compatible with ecosystem-  
94 based management and offers a quantitative assessment of marine ecosystem functioning  
95 (Niquil *et al.*, 2014a; Safi *et al.*, 2019; Heymans *et al.*, 2020). ENAs depict the ecosystem as a  
96 network of interactions, where information can cascade from one part of the network to the  
97 other. Derived from different sciences including economics and thermodynamics (Wulff *et al.*,  
98 1989), ENA indices can quantify emerging properties of ecosystems and monitor their  
99 evolution (Ulanowicz, 1986; Heymans and Tomczak, 2016; Borrett and Scharler, 2019). Using  
100 ENA to spatialize ecosystem models would make them more operational and help marine  
101 spatial planning (Le Tissier, 2020).

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

109 In this study, we propose to investigate the spatial effects of multiple drivers on the Bay  
110 of Seine (eastern part of the English Channel) ecosystem, using ENA indices. This work is based  
111 on the Ecospace model of Halouani *et al.* (2020) modified by Bourdaud *et al.* (2021). It  
112 represents the food web of the extended Bay of Seine (eBoS), and initially modeled the  
113 potential reserve effect of the future offshore wind farm (OWF) of Courseulles-sur-Mer  
114 (Halouani *et al.* 2020). It was also used to explore the potential effects of CC on species  
115 distribution (Bourdaud *et al.* 2021) by combining it with niche models (Ben Rais Lasram *et al.*,  
116 2020).

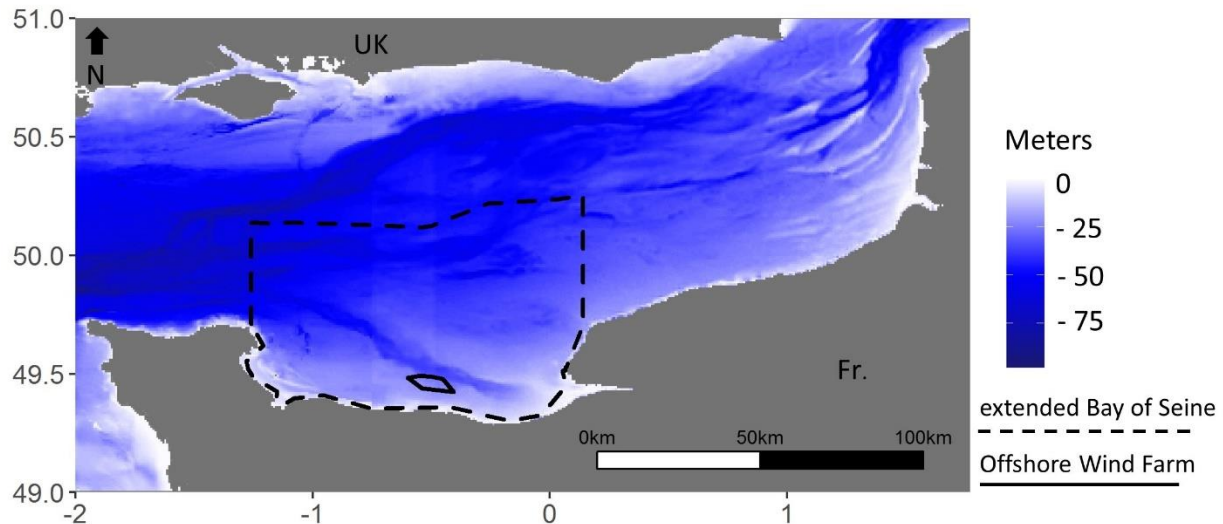
117 Following these works, we integrated new approaches aimed at better forecasting the  
118 possible evolution of the Bay of Seine ecosystem. First, we added the reef effect to the  
119 potential impacts of the future OWF of Courseulles-sur-Mer. Secondly, we used the spatial-  
120 temporal framework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

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

## 132 2 Materials and methods

### 133 2.1 Study area

134 The extended Bay of Seine Ecospace model covers the sea space from the Cotentin  
135 peninsula to Le Havre all the way up to the French-British delimitation of the Exclusive  
136 Economic Zones (Figure - 1). It is a shallow coastal ecosystem open onto the English Channel,  
137 with a mean depth of 35 m varying from 5 m to around 70 m in the paleo-valley north-west of  
138 the eBoS. The eBoS covers 13,500 km<sup>2</sup>; the main sediment types include gravels, coarse sand,  
139 fine sand and muddy fine sand (Supplementary materials Figure S - 1 , Dauvin, 2015).  
140 Oceanographic features include the Seine estuary (south-east of the eBoS), and the Seine  
141 paleo valley (south-east to north-west of the eBoS) (Figure - 1). The Bay of Seine and the  
142 English Channel in general are a highly anthropized ecosystem, with numerous activities  
143 including fishing, aggregate extraction, marine renewable energy, tourism, sea freight and  
144 more (Dauvin, 2015). Fishing is very important in the bay, and more particularly king scallop  
145 (*Pecten maximus*) dredging, but many other fishing techniques are also used. Fishing gears  
146 include trawls and nets targeting demersal fish, trawls targeting small pelagic fish, demersal  
147 fish and cephalopods, as well as other fishing gears (Supplementary materials Table S - 1). The  
148 most harvested fish species include sole (*Solea solea*) and cod (*Gadus morhua*). The bay is also  
149 of great interest for renewable marine energy. The offshore wind farm of Courseulles-sur-Mer  
150 is under construction and should start operating in 2024 (~ 50 km<sup>2</sup>, 64 turbines). Other  
151 offshore wind farm projects of various sizes are also under consideration in the bay.



152

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

156 2.2 Food web modeling

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

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

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

163

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

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

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

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

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

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

185 Finally, Ecospace is a spatially explicit time-dynamic model based on Ecopath and  
186 Ecosim. In Ecospace, the spatial extent of the ecosystem is represented by a grid of cells and  
187 each cell is a time-dynamic trophic model based on Ecosim, with interconnections between  
188 cells (Walters *et al.*, 1999; Christensen *et al.*, 2014). The base map of the eBoS Ecospace model  
189 was made of 4,907 cells, with a resolution of 0.015°x 0.015° each, identified depending on  
190 their row r and their column c (r,c). Input maps included a bathymetric map to define the  
191 model area, extracted from GEBCO (General Bathymetric Chart of the Oceans:  
192 <https://www.gebco.net/>) and a map of primary production from SeaWifs representing the  
193 relative chlorophyll a concentration in the bay in 2000 (<https://podaac.jpl.nasa.gov/>). A  
194 habitat map was used to define species distributions in the initial model of *Halouani et al.*  
195 (2020), but it was replaced with niche model suitability index maps in *Bourdaud et al.* (2021)



196 (Supplementary materials Table S - 3). These suitability index maps were computed using  
197 multi-algorithm niche models (Ben Rais Lasram *et al.*, 2020, Supplementary materials Figure S  
198 - 2 to 28). Niche model algorithms are correlative approaches aimed at identifying the  
199 potential niches of species by correlating species occurrences with environmental variables.  
200 The niche models developed by Ben Rais Lasram *et al.* (2020) used presence-only data  
201 correlated with climatic variables (temperature and salinity) as well as habitat variables (type  
202 of substrate, depth, slope, and orientation). Eight models from BIOMOD were used. Model fit  
203 was determined using a 3-fold cross validation procedure and model performance was  
204 assessed using both the Continuous Boyce Index or CBI and the True Skill Statistic or TSS. Only  
205 the models with an averaged CBI superior to 0.5 were kept (Supplementary materials Table S  
206 4 & 5). All the modeling choices can be found in Ben Rais Lasram *et al.* (2020). Averaged  
207 suitability index maps were then built from the fitted species distribution models, using  
208 climatic and habitat-based species distribution models, and were validated using expert  
209 knowledge.

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

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

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

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

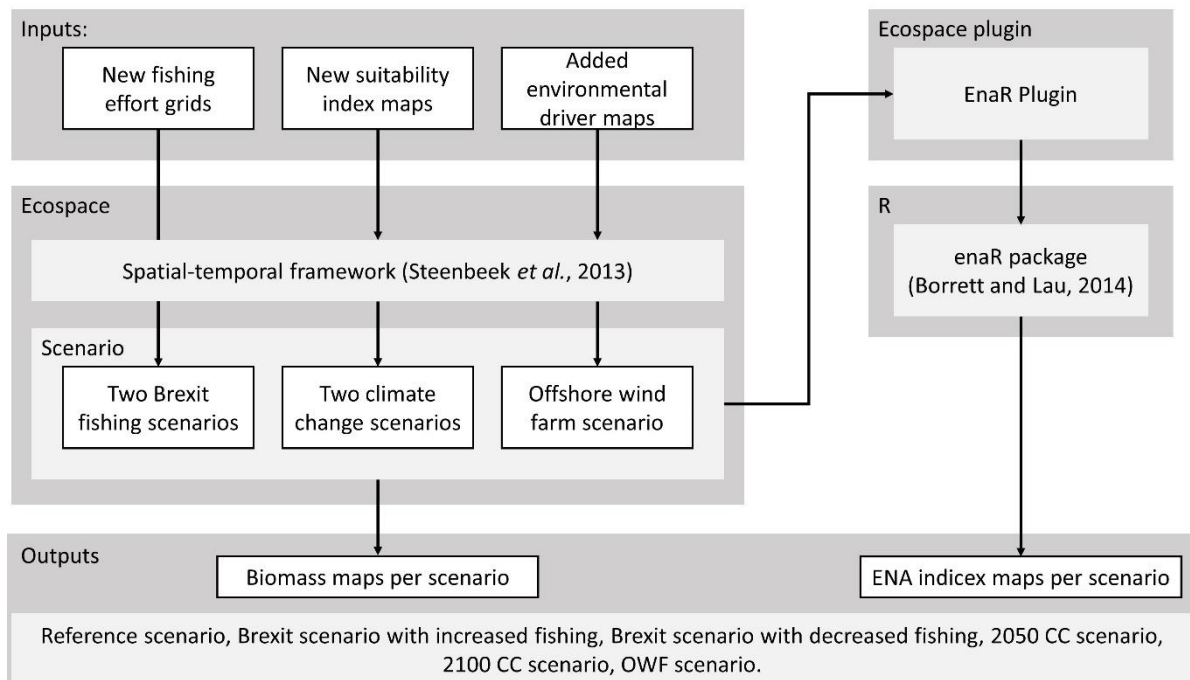
$$V_{ij} = \frac{v_{ij} \cdot B_j}{2 \cdot v_{ij} + a_{ij} \cdot \frac{B_j}{C_{rcj}}} \quad (4)$$

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

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

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

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



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

### 2.3 Effect of climate change on species distribution

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

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

268 have a positive production rate (Hutchinson, 1957), we hypothesized that the production of  
269 the species would be lower close to the limit of the theoretical niche (lower suitability index),  
270 and higher in the center of the theoretical niche (higher suitability index). The niche models  
271 simulated how suitable the geoclimatic parameters were and their evolution by 2050 and  
272 2100, following the IPCC “business as usual” scenario RCP 8.5.

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

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

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

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

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

#### 310 2.4 Fishing scenarios

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

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

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

333 • **F<sub>inc</sub>** considered an increase of fishing in the area resulting from the relocation of  
334 European fisheries from France, Belgium, The Netherlands or even Denmark inside the  
335 eBoS. As European fishermen would not have access to the United Kingdom waters,  
336 they would have to fish in other places, e.g. in the eBoS. King scallop fishing would still  
337 be reduced, as no new quotas are likely to be set to let other countries take up the  
338 UK’s vacant place, even though some French fishermen could benefit from it. In our  
339 scenario, this resulted in a 20 % increase of the “pelagic and bottom trawls”, the  
340 “bottom trawls” and the “pelagic trawls” activities, as well as a 5 % increase of “other  
341 fishing gears” activities based on the previous Brexit scenario.

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

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

#### 349 2.5 Offshore wind farm

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

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

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

370 Due to the small footprint of the OWF foundation compared to the Ecospace cell  
371 resolution (5% of a single cell), modeling the reef effect was not possible by simply changing  
372 the habitats in the cells. We had to look at a previous model of the reef effect of the  
373 Courseulles-sur-Mer OWF (Raoux *et al.*, 2017). The observations on this Ecopath model were  
374 linked to the 70 km<sup>2</sup> farm in Ecospace (37 cells). In Raoux *et al.* (2017), the reef effect was  
375 modeled by forcing the biomass of 10 trophic groups and the replacement of soft sediment  
376 by hard substrates was thus considered insignificant. We did the same by creating new  
377 environmental maps for the same groups in the eBoS Ecospace model to represent the  
378 biomass variations caused by the reef effect (Supplementary materials Table S - 9). The  
379 increased habitat suitability due to the reef effect would thus lead to a higher foraging capacity  
380 based on the foraging arenas theory (Walters *et al.*, 1997; Ahrens *et al.*, 2012). The new  
381 environmental maps were added using the spatial-temporal framework of Ecospace at the  
382 2015 time step, before the CC simulations. Similar structural sub-regions were used to  
383 characterize the effects of the OWF on the eBoS ecosystem (Halouani *et al.* 2020): the OWF  
384 area itself, the first two rows of cells surrounding the farm (spillover 1), the next two rows of  
385 cells surrounding the farm (spillover 2) and the rest of the eBoS model (Bay) (Supplementary  
386 materials Figure S - 35).

387 2.6 Ecological network analysis

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

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

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



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

398

## 399 2.7 Statistical analysis

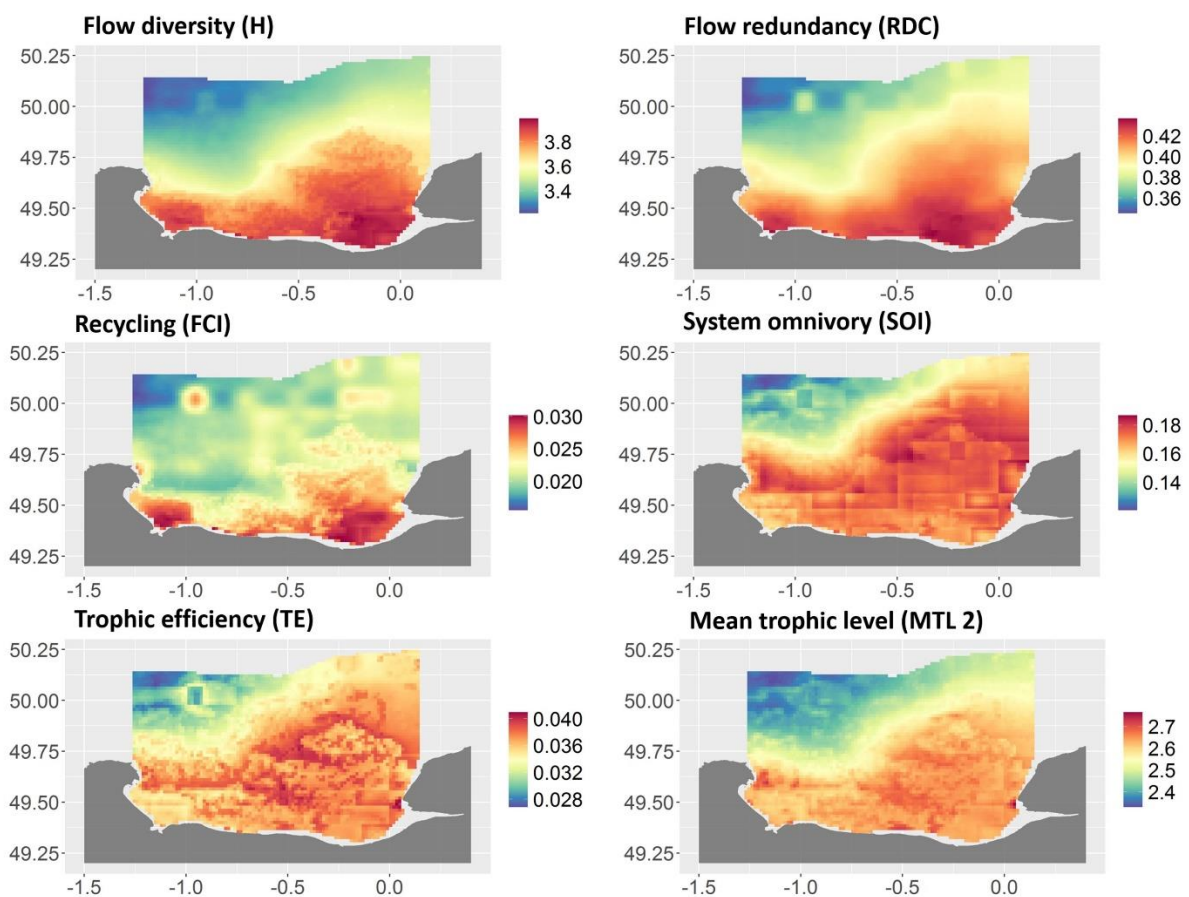
400 In order to better understand the effects of each scenario spatially, a K-means clustering  
 401 analysis was carried out (MacQueen, 1967) on the ENA results of the current reference  
 402 scenario. The “Elbow” method was used to determine the optimal value of the cluster based  
 403 on multiple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

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

## 413 3 Results

### 414 3.1 Regionalization of the model

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

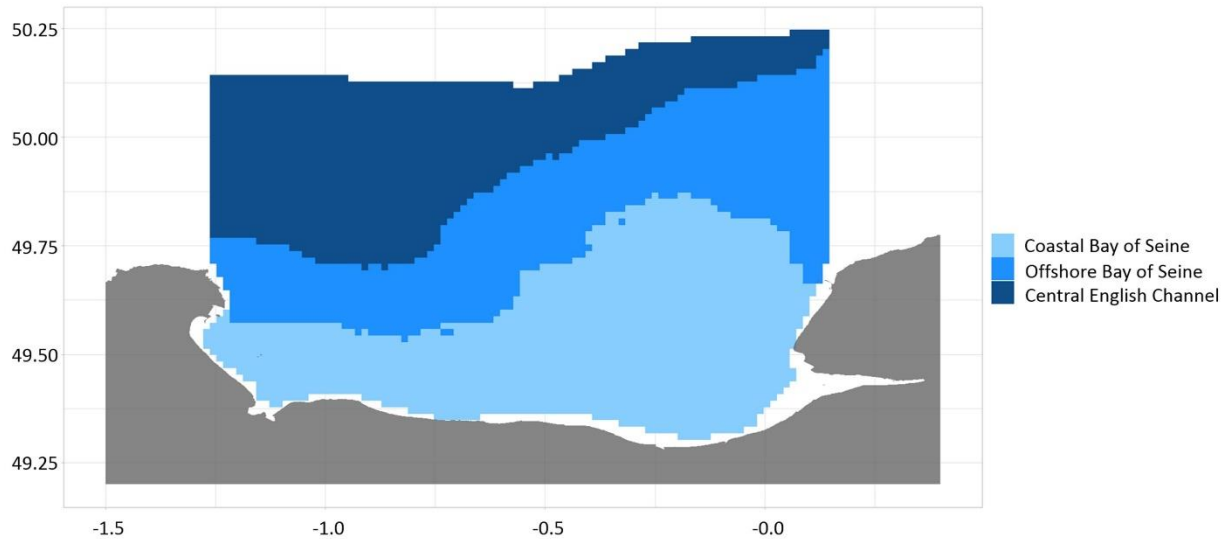


422

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

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

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



431

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

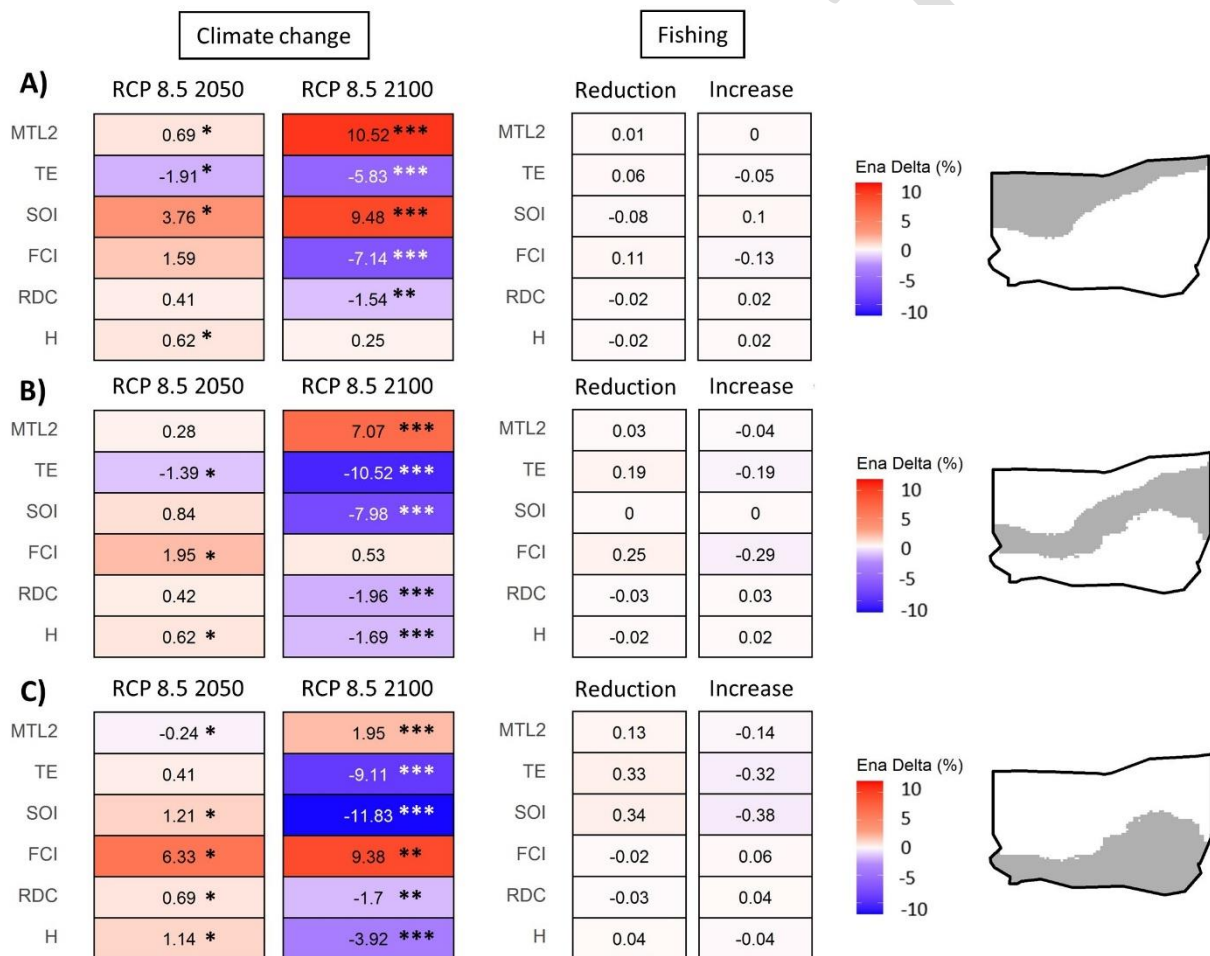
435 3.2 Effects of climate change and fishing on the functioning and organization of the  
436 system

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

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

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

454 In general, the Coastal Bay of Seine region was the most sensitive area to CC (in both the  
 455 2050 and 2100 scenarios), with negligible variation of only one of its ecological indices,  
 456 followed by the Central English Channel (3 indices) and finally the Offshore Bay of Seine (4  
 457 indices).



458

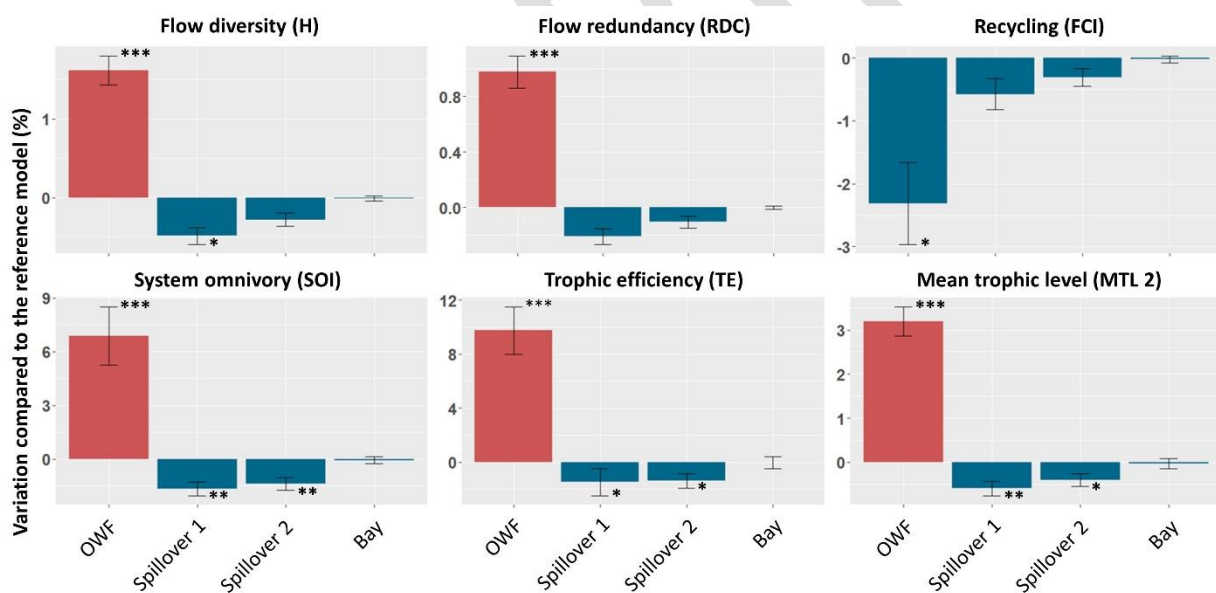
459 **Figure - 5 Variations between the reference scenario and the different CC**  
 460 **scenarios (left columns) and Brexit scenarios (right columns).**

461 Positive variations are in red boxes, and negative variations in blue  
 462 boxes. A), variation in the Central English Channel region; B), variation in the  
 463 Offshore Bay of Seine region; C), variation in the Coastal Bay of Seine region.  
 464 Cliff Delta results: \*\*\* strong variation ( $|\partial\text{Cliff}| > 0.474$ ); \*\* medium

465 variation ( $0.33 < |\partial\text{Cliff}| < 0.474$ ); \* small variation ( $0.147 < |\partial\text{Cliff}| <$   
466  $0.33$ ); no \*, negligible variation ( $|\partial\text{Cliff}| < 0.147$ ).

### 467 3.3 Effect of the offshore wind farm on the system

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



478

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

481 Regions include the spillover 1 region (first two rows of cells around  
482 the OWF), the spillover 2 region (next two rows of cells around the OWF)  
483 and the rest of the bay. All sub-regions are exclusive, with no overlapping.  
484 Red bars, positive variations; blue bars, negative variations. Cliff Delta  
485 variation: \*\*\* strong ( $|\partial\text{Cliff}| > 0.474$ ); \*\* medium ( $0.33 < |\partial\text{Cliff}| <$   
486  $0.474$ ); \* small ( $0.147 < |\partial\text{Cliff}| < 0.33$ ); no \*, negligible ( $|\partial\text{Cliff}| < 0.147$ ).

487 4 Discussion

488 The modeling approach implemented in the present study improved the simulation of  
489 multiple drivers, using whole ecosystem approaches based on a single reference model. We  
490 did not represent the entire effect of CC, but rather tried to progressively improve the  
491 forecasting previously achieved in the Bay of Seine (Bourdaud *et al.*, 2021; Halouani *et al.*,  
492 2020; Nogues *et al.*, 2020; Raoux *et al.*, 2019). Despite improvements such as modeling the  
493 reef effect of the OWF, modeling the effects of climate change on species physiology (through  
494 the habitat capacity), adding variability in the fishing regimes, there still remains limitations  
495 related to the great complexity of climate change and of its impacts on ecosystems (Hoegh-  
496 Guldberg and Bruno, 2010; Ainsworth *et al.*, 2011). Such limitations include the failure to  
497 account for the arrival of tropical non-indigenous species (NIS) in the eBoS (Cheung *et al.*,  
498 2009; Weatherdon *et al.*, 2016). Modeling the inflow of non-indigenous species due to CC in  
499 an open system like the Bay of Seine is a very hard task. The results are often hypothetical and  
500 subject to many modeling hypotheses (Morin and Thuiller, 2009; Beaugrand *et al.*, 2018; Le  
501 Marchand *et al.*, 2020). Moreover, the arrival of non-indigenous species is often modeled with  
502 new trophic groups (Libralato *et al.*, 2015; Corrales *et al.*, 2018), which change the system  
503 aggregation. Comparing the system before and after the arrival of NIS using ecological  
504 network analysis becomes tricky, as some ENA indices are highly sensitive to the system  
505 aggregation (Johnson *et al.*, 2009). That is why we chose not to integrate such arrivals for the  
506 time being, even though NIS might have several effects on the food web structure (Libralato  
507 *et al.*, 2015; Kotta *et al.*, 2018).

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

517 dynamics of local macro-organisms and its effects on the ecosystem functioning (Harley *et al.*,  
518 2006).

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

530 4.1 Climate change and species distribution: consequences on food web functioning

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

546 to play a major role in the future evolution of marine ecosystems (Walther *et al.*, 2002;  
547 Parmesan, 2006).

548 The structuring effect of climate change in the 2100 RCP8.5 scenario seems to result  
549 from important community changes that lead to a lower resistance of the system to  
550 disturbances. Community changes are visible through the increased mean trophic level of the  
551 system and coincide with decreased benthic invertebrate biomass as well as modified fish  
552 biomass (Supplementary materials Figure S - 41). This is the result of the high sensitivity of  
553 multiple benthic invertebrates species to CC (Rombouts *et al.*, 2012), as well as the high  
554 vulnerability of low-trophic-level fish to changing climate conditions (McLean *et al.*, 2018),  
555 making them potentially highly sensitive to CC. Taken together, the decreased biomass of low  
556 trophic level groups like invertebrates and small fish will reduce the mean trophic level and  
557 result in a loss of redundant trophic pathways, leading to a lower relative redundancy of the  
558 flow in the system. Such changes have been related to losses in the ability of the system to  
559 adequately respond to external pressure by reconfiguring itself (Odum, 1985; Ulanowicz,  
560 1986). Losing this ability makes a system less resilient to stressors, as described by Heymans  
561 and Tomczak (2016). It is well known that invertebrates are going to be highly impacted by CC  
562 (Kendall *et al.*, 2004; Byrne, 2011). However, few studies have investigated the overall effect  
563 of community changes on ecosystem functioning. Our results support the idea that benthic  
564 communities could play a major role in the resilience of the eBoS ecosystem (Nogues *et al.*,  
565 2020; Raoux *et al.*, 2019).

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



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

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

592 Although CC effects in the 2050 scenario are less visible than in the 2100 scenario, local  
593 trends can still be outlined. While the model forecasts a decrease of the mean trophic level in  
594 the Coastal Bay of Seine region, an increased mean trophic level is expected in the Central  
595 English Channel region. This gradient can be explained by the increase of invertebrate biomass  
596 values in the most coastal region, increasing flow redundancy and recycling (Supplementary  
597 materials Figure S - 42). In the more offshore Central English Channel region, a loss of  
598 invertebrate biomass results in a decreased invertebrate / fish ratio (Supplementary materials  
599 Figure S - 42). This modification of the ecological communities is noticeable at the ecosystem  
600 level *via* a higher mean trophic level and a lower trophic efficiency. While the 2100 scenario  
601 appears to be impacted both globally (at the entire eBoS scale) and locally (inside the eBoS),  
602 the impact of CC seems more local in the 2050 scenario with no homogeneous effects at the  
603 entire eBoS scale. This is why it is crucial to take the effects of CC into account both globally  
604 and locally. Detecting such effects at the community level might be an issue for many local  
605 development actors as they prefer to use “tailor-made” solutions, specific to their case study,

606 that may fail to detect holistic ecosystem changes (Hendriksen *et al.*, 2014). ENA showed that  
607 by using a spatialized model, they could characterize and understand the effects of CC on the  
608 ecosystem between functional regions (local effects) and across the whole eBoS (global  
609 effects). This represents a societal priority for us to be able to predict the evolution of marine  
610 ecosystems (Claudet *et al.*, 2020). Information about the local effect of CC could prompt local  
611 stakeholders to set up actions in the field of vulnerability and adaptation of the societal system  
612 (Charles, 2012) and to raise awareness at a local scale (Ireland and Clausen, 2019).

#### 613 4.2 ENA indices in fishing scenarios

614 While the effects of CC on the ecosystem are not proportional between the 2050 and  
615 2100 scenarios, with strong but sometimes completely different effects on some indices,  
616 fishing has negligible but proportional effects, opposite in the two Brexit scenarios (fishing  
617 increase / decrease). The trophic efficiency and the mean trophic level have already been used  
618 in many studies to describe the effect of fishing on the ecosystems (Libralato *et al.*, 2004, 2010;  
619 Coll *et al.*, 2009). On the other hand, the mean trophic level was popularized by Pauly *et al.*  
620 (1998) and his “Fishing down the marine food web” theory that depicts the mean trophic level  
621 as sensitive to the effect of fishing, i.e. decreasing with the fishing pressure due to the  
622 decreased predator biomass. The omnivory index was also promoted as a robust index to  
623 detect the effect of fishing (Fulton *et al.*, 2005). Despite the many items of evidence of their  
624 operational ability to describe the effects of fishing, ENA variations due to fishing were  
625 consistently considered negligible by the Cliff Delta. The little sensitivity of ENA indices to  
626 fishing scenarios might thus result from the little impact of the Brexit scenario on ecosystem  
627 functioning. The eBoS is a heavily anthropized ecosystem, with a strong fishing industry  
628 (Buléon and Shurmer-Smith, 2021). Protecting the ecosystem from the effects of fishing might  
629 require ambitious management plans to truly help ecosystems recover (Dunford *et al.*, 2004).

#### 630 4.3 Effect of the offshore wind farm on the extended bay of Seine

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

636 flows. The aggregating effect is also noticeable outside the OWF perimeter. Biomass outside  
637 the OWF appears lower in the OWF eBoS scenario than in the reference scenario. This  
638 decreased fish biomass is likely due to the agglomeration of the mobile fish groups inside the  
639 OWF area due to the higher suitability of the cells and to the higher prey density for fish groups  
640 inside the OWF. Agglomeration is well known and has been extensively studied (Bohnsack,  
641 1989; Pickering and Whitmarsh, 1997; Smith *et al.*, 2015) and was also observed by Halouani  
642 *et al.* (2020) to be caused by the reserve effect only (Colléter *et al.*, 2014).

643 Inside the OWF perimeter, Ecospace predicted a similar structuring effect to the one  
644 forecasted in Nogues *et al.* (2020). This structuring effect is visible through the many  
645 important modifications of the ecosystem, which appears to shift toward a more demersal /  
646 benthic system (Supplementary materials Figure S - 45). Similarly to the results of Raoux *et al.*  
647 (2019), the OWF could increase the relative redundancy of the flow. The OWF of the eBoS  
648 model may also increase the omnivory index of the system, as observed by Nogues *et al.*  
649 (2020). However, unlike previous studies, recycling is reduced by the OWF in our simulations.  
650 All these modifications – along with the increased trophic efficiency and the increased flow  
651 diversity – seem to be linked to an increased resistance of the system to disturbance. With the  
652 higher flow redundancy, the system has more in store against disturbances (Levin and  
653 Lubchenco, 2008), improving its ability to adapt and overcome stresses. The higher omnivory  
654 index also suggests that the system would be more resilient, as it makes it more flexible  
655 (Fagan, 1997; Libralato, 2013). The heterogeneity brought by the hard substrate of the wind  
656 turbine structure to the sandy habitat surrounding the OWF seems to increase the flow  
657 diversity. Flow diversity can be interpreted as species diversity (Christensen, 1995). Therefore,  
658 an increase in habitat heterogeneity should also increase local diversity (Munguia *et al.*, 2011).  
659 These changes are all linked to the increase in benthic and demersal biomass (Supplementary  
660 materials Figure S - 45), which tends to have an overall positive impact on the ecosystem of  
661 Courseulles-sur-Mer by making it more complex, efficient, diverse and resilient (Nogues *et al.*  
662 2020).

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

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

## 679 Conclusion

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

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## 703 **Data availability statement**

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

## 706 **Author contribution**

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

## 710 **Competing interest statement**

711 The authors have no conflict of interest to declare.

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