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1 **Measuring sensitivity of two Ospar indicators for a coastal food web model under Offshore**  
2 **Wind Farm construction**

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21 **ABSTRACT**

22 A combination of modelling tools was applied to simulate the impacts of the future Courseulles-sur-mer  
23 offshore wind farm construction (OWF) (Bay of Seine, English Channel) on the ecosystem structure and  
24 functioning. To do so, food-web models of the ecosystem under three scenarios were constructed to  
25 investigate the effect of added substrate (reef effect), fishing restriction (reserve effect), and their combined  
26 effect caused by the OWF. Further, Ecological Network Analysis indices and Mean Trophic Level (MTL) were  
27 derived to investigate their suitability for detecting changes in the ecosystem state. Our analyses suggest  
28 changes in the ecosystem structure and functioning after the OWF construction, the ecosystem maturity was  
29 predicted to increase, but no alterations in its overall resilience capacity.

30

31 **KEYWORDS:** Ecopath with Ecosim; Ecological Network Analysis; reef effect; reserve effect; Mean Trophic  
32 Level; Marine Renewable Energy.

33 **1. INTRODUCTION**

34 In order to reduce carbon emissions, there is a worldwide transition of the energy production scheme from  
35 fossil fuels to renewable energy sources. Furthermore, there is currently in Europe a strong political drive for  
36 the development of Marine Renewable Energies (MRE). For instance, the European Union (EU) Renewable  
37 Energy Directive (2009) has set a common target for 20% of EU's energy to come from renewable sources by  
38 2020. As a consequence, the development of Offshore Wind Farm (OWF) projects along the coast of France  
39 is rapidly increasing. Three successive calls for tenders related to OWF development have been successively  
40 announced, and seven sites have been selected for future OWF construction. Among them, three should be  
41 built in the Eastern English Channel: in Fécamp, Dieppe-LeTréport, and Courseulles-sur-mer. Beyond the fact  
42 that the English Channel is the current hotspot for OWF development in France (Raoux et al., 2017), it is also  
43 a significant economic area already subjected to multiple anthropogenic perturbations such as pollution,  
44 transport, fishing, aquaculture, aggregate extraction, and sediment dredging and deposit (Dauvin, 2012;  
45 2015).

46 Development of OWF installations across the Eastern English Channel will lead to the introduction of hard  
47 substrates in the natural soft sediments, which is expected to cause changes in the benthic community in the  
48 vicinity of the turbines (Coates et al., 2014). In fact, these hard substrates are likely to be used directly as  
49 habitats by several epibenthic and benthic species, and to attract a new suits of species, including non-native  
50 ones (Wilhelmsson and Malm, 2008; Maar et al., 2009). Previous studies made in the Baltic and North seas  
51 showed that filter feeders such as mussels and amphipods tended to dominate on the turbine vertical  
52 structures, while benthic predators such as crabs dominate on the foundation base and the score protections  
53 (Wilhelmsson et al., 2006; Krone et al., 2017). This aggregation of epibenthic and benthic organisms on the  
54 turbine foundations is known as the "reef effect" and is considered as one of the most important effects on  
55 the ecosystem generated by OWF construction (Petersen and Malm, 2006; Langhamer, 2012). Besides the  
56 "reef effect", spatial restrictions in form of fisheries exclusion zones (e.g. bottom trawl and dredge) are likely  
57 to be implemented around turbines and cables for navigation safety. These two fishing activities are known  
58 to be major threats to benthic organisms and their associated habitats (Thurstan et al., 2010; Turner et al.,  
59 1999). A possible exclusion of fishing activities inside the OWFs could act as local Marine Protected Areas  
60 (MPAs) (Shields et al., 2014). MPAs are known to cause "reserve effect" which can lead to increased local  
61 biomasses (Leonhard et al., 2011; Lindeboom et al., 2011; Shields et al., 2014) and possible changes in the  
62 food-web structure. However, until now, it has seemed difficult to separate effects of fisheries exclusion from  
63 the "reef effect" in field (Bergström et al., 2014). Clearly, solutions set to mitigate the impacts of climate  
64 change will have consequences on biodiversity and ecosystem functioning. Therefore, an important  
65 challenge for the scientific community is now to assess the range of the possible ecological consequences  
66 before project implementations (or decisions) to optimize the targeted objectives. The Marine Strategy

67 Framework Directive (MSDF) (EU, 2008) stresses the urgent need of development, tests and validation of  
68 ecosystem health indicators. The ecosystem approach is explicitly developed and applied with the aim of  
69 attaining Good Environmental Status (GES) of ecosystems. The directive's recent revision (EU, 2017) has even  
70 emphasized the importance of considering marine ecosystem's structure, functions and processes to  
71 achieving GES. Further, MSFD has suggested to develop more integrative and process-oriented food-web  
72 indicators (Rombouts et al., 2013). The OSPAR convention (an international cooperation on the marine  
73 environmental protection of the North East Atlantic) has proposed a list of food-web indicators which would  
74 capture the emerging properties of the food web (Niquil et al., 2014). The ENA indices are among these  
75 indicators, but they are not yet considered as "operational" and cannot be used in the assessment of the  
76 marine environmental status.

77 For several years, the "reef effect" has only been investigated on benthic and fish species alone, but never  
78 with a holistic approach to assess its potential impacts on the ecosystem taken as a whole. Recently, Raoux  
79 et al. (2017) explored a new way to look at the potential impacts of OWFs through food-web models and  
80 flow analysis. They used the Ecopath with Ecosim (EwE) approach (Polovina, 1984; Christensen and Walters,  
81 2004; Christensen et al., 2008) to model the trophic web at Courseulles-sur-mer OWF site. This approach, in  
82 which all biotic components of the system can be considered at the same time, is useful to gain a better  
83 understanding of the ecosystem structure and functioning, and for predicting how it may change over time  
84 when facing perturbations (Plagányi, 2007). Then, Raoux et al. (2017) used the Ecosim model (the temporal  
85 dynamic module of EwE) to project the evolution of the ecosystem over the next 30 years after an expected  
86 increase in biomass of some targeted benthic and fish compartments in relation to the OWF construction.  
87 Ecological Network Analysis (ENA) indices (Ulanowicz, 1986) were further calculated, summarising the  
88 emergent properties of the ecosystem, giving indications about the possible state of the ecosystem at the  
89 end of the simulation. Among the core conclusions were (1) that the total ecosystem activity, the overall  
90 system omnivory, and the recycling should increase after the OWF construction, and (2) that some higher  
91 trophic levels (i.e. exploited piscivorous fish species, endangered marine mammals) are very likely to respond  
92 positively to the biomass aggregation on the scour protections of the piles and turbines. Even if the study of  
93 Raoux et al. (2017) strongly suggested that the ecosystem structure and functioning would experience  
94 changes in response to the OWF construction, before/after statistical comparisons were not possible as  
95 outputs from the Ecopath model and Ecosim simulation were only providing one value per ENA index. The  
96 authors emphasized the need to quantify the uncertainty in the ENA indices in order to produce robust  
97 conclusions on the ecosystem functioning, and thereby better predict its responses to disturbances.

98

99 The objective of the current study was to investigate the usefulness of ENA indices in the assessment of the  
100 state of the ecosystem by confronting them to a complementary indicator developed under the OSPAR  
101 commission, the Mean Trophic Level (MTL), which is considered as operational and was used in the OSPAR  
102 2017 intermediate assessment ([www.ospar.org](http://www.ospar.org)). Following the modelling procedure in Raoux et al. (2017),  
103 the present study is intended to further deepen our understanding of the OWF construction effect on the  
104 ecosystem by:

- 105 • the increase in number of plausible scenarios: simulations of both the “reef effect” and the “reserve  
106 effect” on the ecosystem will be performed, as well as their combined effect;
- 107 • the comparison of ENA indices to “traditional” indicators such as MTL;
- 108 • the quantification of the uncertainty in the ENA indices: this will strengthen our interpretation of  
109 these indices by allowing to statistically test the differences between the scenarios in terms of  
110 predicted ecosystem functioning. This will be performed using the ENAtool routine generating  
111 probability distributions for ENA indices at the end of each simulation run (Guesnet et al., 2015);
- 112 • discussing our results in the scope of the theory of ecological stability (Holling, 1996)

## 113 **2. MATERIAL AND METHODS**

### 114 **2.1 Study area**

115 The OWF will be built in the next years in the Bay of Seine (English Channel eastern part) which forms a  
116 roughly 5000-km<sup>2</sup> quadrilateral. The Bay of Seine never exceeds 30 m in depth. The maximum speed of the  
117 tidal currents is around 3 knots in the north of the bay (Salomon and Breton, 1991; 1993). The tidal currents  
118 play an important role in distributing both sediments and benthic communities (Larsoner et al., 1982; Gentil  
119 and Cabioch, 1997). The dominant offshore sediments are pebbles, gravels and coarse sands, while the  
120 inshore sediments are mostly fine sands and muddy fine sands (Dauvin et al., 2007; 2015).

### 121 **2.2 Courseulles-sur-mer Offshore Wind Farm**

122 The Courseulles-sur-mer OWF will be located 10 to 16 km offshore from the Calvados coast at a depth of 22  
123 to 30 m. It will be located on the coarse sand and pebbles benthic communities of the Bay of Seine (Fig. 1).  
124 The OWF will represent an area of 50 km<sup>2</sup>. The 75 turbines (each 6 MW) capable of producing 450 MW will  
125 be installed by Eoliennes Offshore du Calvados” (EOC) (a subsidiary of Éolien Maritime France (EMF) and wpd  
126 Offshore) in the next years.

127 In the Environmental Impact Assessment (EIA), EOC proposed two scenarios. In the first scenario, the 75  
128 monopiles and the converter station will require scour protections. In addition, 33% of the cables will be

129 rock-dumped. In the second scenario, 7.6 km<sup>2</sup> or up to 15% of the total surface of the Courseulles-sur-mer  
130 OWF will be closed to fishing for safety measures. Thus, the active gears will be banned 150 m around the  
131 cables whereas the passive gears will be not banned around them and both the passive and active gears will  
132 be banned around the substation.

133 <Figure 1>

### 134 **2.3 The pre-existing Ecopath model**

135 The Ecopath with Ecosim (EwE) approach was retained by Raoux et al. (2017) to estimate the value of all  
136 carbon flows in the food-web at the Courseulles-sur-mer OWF site. This Ecopath model was composed of 37  
137 compartments, from primary producers (phytoplankton) to top predators (seabirds). The calculated Pedigree  
138 index for this model called model “Before the implantation of the OWF” or BOWF was 0.523.

139

140 Details about the functional group composition, a detailed description of the Ecopath with Ecosim approach  
141 (Christensen and Walters, 2004; Christensen et al., 2008), and the main equations are given in Raoux et al.  
142 (2017).

### 143 **2.4 Time dynamic simulations: the “reef effect” and “reserve effect” due to the OWF implantation**

144 Ecosim is the EwE temporal module which allows to re-calculate the initial Ecopath snapshot model for each  
145 time-step, taking into account a series of variations in the input parameters such as fishing effort or biomass  
146 accumulation. In this study we analysed three different scenarios using EwE. For the first scenario, we used  
147 the work by Raoux et al. (2017), who ran the Ecosim module to analyse the potential impacts on the  
148 ecosystem of benthic and fish aggregations inside the OWF ecosystem (REEF scenario). In the REEF scenario,  
149 expected biomasses were calculated for species that would presumably profit from the “reef effect” (Koller  
150 et al., 2006; Reubens et al., 2011; Krone et al., 2013; Reubens et al., 2013) by multiplying the average biomass  
151 per m<sup>2</sup> found in the literature for the respective species by the surface area represented by the turbine  
152 foundations and scour protections, and divided by the total OWF area. A temporal simulation was then run  
153 over 30 years while forcing the biomasses to increase for the targeted species compartments, and while  
154 keeping the original biomass values for the other functional groups. At the end of the simulation, an Ecopath  
155 model was derived and ecosystem flows and indices were calculated. More details are given in Raoux et al.  
156 (2017).

157 In the present study, the same methodology as in Raoux et al. (2017) was followed for the REEF scenario.  
158 But, two more scenarios were applied: (1) by decreasing the fishing pressure (OPTIM scenario) in accordance  
159 with what is proposed by the OWF owners in the EIA in order to “optimize” the area for fishing activities; (2)

160 by combining the REEF scenario developed by Raoux et al. (2017) and the OPTIM scenario developed in this  
161 study into one (COMBINED scenario).

162

163 For the OPTIM scenario, a temporal simulation was run over 30 years with a reduction in fishing pressure  
164 inside the OWF. In this scenario, 7.6 km<sup>2</sup> or 15% of the total surface of the Courseulles-sur-mer OWF was  
165 closed to fishing. Landings of species that would presumably profit from this decrease in fishing pressure,  
166 such as king scallop, European plaice, sole, other flat fish, sea bream, pouting, Atlantic cod, sharks and rays,  
167 European sea bass, mackerel, benthic and benthopelagic cephalopods were changed accordingly. The Ecosim  
168 model was run with the new landings values (-15 % of the initial landing values of the BOWF model) for the  
169 targeted groups listed above as the only variations taken into account to drive the evolution of the system  
170 through time. Benthic and fish catches were obtained from the IFREMER Fisheries Information System  
171 (<http://sih.ifremer.fr/>). For more information about the landing data please see Raoux et al. (2017).

172 For the COMBINED scenario, we combined the assumptions from the REEF and the OPTIM scenarios, as  
173 detailed above.

174 For these two new scenarios, we extracted, from the Ecosim simulation, a new Ecopath model at the end of  
175 the 30 years' simulations, to compare the situation described in the BOWF model to the one after the  
176 construction of the OWF (OPTIM and COMBINED simulations). We followed the same balancing procedure  
177 as presented in Raoux et al. (2017).

## 178 **2.5 Linking ecosystem health with two types of OSPAR indicators**

179 Recently, there has been a growing interest and need for robust ecological indices to evaluate ecosystem  
180 status. Several indicators are being developed by the OSPAR Commission to protect and conserve marine  
181 ecosystems. These include the Mean Trophic Level (MTL) which has been adopted as a common indicator  
182 (i.e. commonly adopted by several OSPAR Member States) and the ENA indices which are candidate  
183 indicators (i.e indicators that are still being developed and tested prior to potential adoption by OSPAR  
184 Member States). In the current study, the suitability of ENA indices to assess the ecosystem's state was  
185 investigated, confronting them to two other OSPAR indicators, namely the Mean Trophic Level and the  
186 Biomass of the Groups.

187

188 **2.5.1 OSPAR common Indicator (The Mean Trophic Level)**

189 The MTL, an indicator from the OSPAR food-web list of indicators (Niquil et al., 2014), was used to describe  
190 changes in the structure of the food web following the OWF construction. Using outputs of functional groups'  
191 biomass and trophic levels derived from the three scenarios, MTL was calculated as the weighted average  
192 trophic level for functional groups following the equation:

193 
$$MTL = \frac{\sum_i TL_i B_i}{\sum_i B_i} \quad (\text{Eq. 1})$$

194 where  $TL_i$  and  $B_i$  are the trophic level and the biomass of each functional group, respectively. According to  
195 Shannon et al. (2014), three MTL were calculated for each scenario, in order to capture (1) the whole  
196 community of consumers (MTL\_2.0) with a cut-off of functional groups with a Trophic Level (TL) < 2 (i.e:  
197 primary producers and detritus were not taken into account); (2) the higher trophic levels species (MTL\_3.25)  
198 excluding functional groups with TL < 3.25; and (3) the top predators (MTL\_4.0) excluding functional groups  
199 with TL < 4.0.

200 **2.5.2 Candidate Indicators (the Ecological Network Analysis indices)**

201 Ecological Network Analysis indices (ENA, Ulanowicz, 1986) were used to compare the ecosystem structure  
202 and function before and after the OWF installation. The following structural ENA indices namely Total System  
203 Throughput (T., Latham, 2006), Ascendency (A, Ulanowicz, 1997, relative Ascendency (A/C, Ulanowicz et al.,  
204 2009), Redundancy (Ulanowicz, 1986; 1997), relative redundancy (R/C, Ulanowicz et al., 2009), System  
205 Omnivory Index and Transfer Efficiency (TE, Lindeman 1942) as well as the following functional ENA indices  
206 namely Finn's Cycling Index were retained (FCI, 1980). More details were given in Raoux et al. (2017).

207 Finally, two more ecosystem attributes were characterized by the following ratios: the total primary  
208 production/total respiration (PP/R) and total biomass/total system throughputs (B/T..)

209 The network analysis plug-in included in EwE (Christensen and Walters, 2004) was used to calculate the ENA  
210 indices for the BOWF, REEF, OPTIM and COMBINED models.

211 **2.6 Statistical analysis on the ENA indices**

212 Ecopath is a single solution model and so statistical comparisons between models were not possible. The  
213 ENAtool routine (Guesnet et al., 2015) was built to incorporate uncertainty around input parameters and  
214 provided ENA index distributions that can be statistically compared between models. This tool is resampling  
215 multiple balanced input matrices and calculating a set of ENA indices for each one. To do so, for each input

216 parameter of the BOWF Ecopath model, an uncertainty interval based on the EwE pedigree routine was  
217 allocated. In fact, EwE presents a pedigree routine that allows modellers to quantify the input parameter  
218 quality and associates a confidence interval according to predefined tables (Christensen and Walters, 2004).  
219 Here, a set of 50 balanced models were sampled with input parameters boundaries defined as in Table 1.  
220 The same was completed with the REEF, OPTIM and COMBINED models. As the models were highly  
221 constrained (i.e. EE close to 0.99 for many groups), computational time to generate balanced input matrices  
222 was extremely high. As such, the set was limited to 50 in the present study which corresponded already to  
223 several millions of trials to obtain the number of solution obeying our constraints. As probability distributions  
224 were generated for each index in the four models, it was now possible to test the significance of differences  
225 between models.

226 <Table 1>

227 Considering that the ENA indices distributions generated by the ENAtool routine were unpaired, statistical  
228 differences between these ENA indices distributions of the BOWF model and the three scenarios were  
229 obtained by testing whether ENA indices means differed from zero following permutation tests. In fact, the  
230 permutation method is a non-parametric test which means that unlike popular parametric test like ANOVAs,  
231 it does not make specific assumption about the shape of population distribution from which the observation  
232 has been derived (Groope et al., 2011). It assumes only that the observation is exchangeable. Thus, ENA  
233 indices distributions were randomized across the model and the three scenarios. However, as we tested  
234 several times the same hypothesis for non-independent indices, the maximum-statistic method for multiple  
235 comparisons (also called minimal p-value method for multiple comparisons) (Nichols et al., 2003; Gropppe et  
236 al., 2011). This method, like Bonferroni correction, allows to control the probability that one or more false  
237 discoveries is made during the multiple comparison (Groope et al., 2011). It also allows to take into account  
238 the multiplicity of testing but also to keep the correlation structure between the indices. With this method,  
239 all the indices were compared at the same time (multiple comparisons). For that, each ENA indices was  
240 standardized by removing by its mean and by dividing its standard deviation, thus the unit of all the ENA were  
241 the same. One thousand randomization samples were carried out. Significant values were then determined  
242 by comparing the distributions obtained to the ENA indices means before randomization. Results are  
243 presented in Table 3, significant value ( $pvalue < 0.05$ ) are indicated in bold.

### 244 **3. Results**

245 The ecosystem structure and functioning before OWF construction (i.e. BOWF model) have already been  
246 described in Raoux et al. (2017). The BOWF model and the REEF scenario were used unchanged in the present  
247 paper. The 4 balanced trophic webs included 37 functional groups.

248 **3.1 Trophic levels and biomass profiles**

249 The trophic levels of the functional groups ranged from TL=1 for primary producers and detritus, to a  
250 maximum of 4.8 represented by marine mammals (i.e. by grey seals in the BOWF model and OPTIM scenario,  
251 and by bottlenose dolphins in the REEF and COMBINED scenarios) (Table 2). Most functional groups  
252 maintained approximately the same trophic level between the different scenarios.

253 The biomass by trophic levels exhibited a similar pattern between the BOWF model and the three scenarios,  
254 with the majority of the biomass being concentrated at TL 2 (Table 2). These high biomasses were mainly  
255 related to bivalves in the BOWF model and the OPTIM scenario, and more specifically, to bivalves and benthic  
256 predators in the REEF and COMBINED scenarios. The REEF and COMBINED scenarios exhibited also a higher  
257 biomass of benthic invertebrates compared to the BOWF model and the OPTIM scenario.

258 A comparison between the compartmental throughflows (the amount of energy going through a  
259 compartment in terms of carbon) between the BOWF model and the three simulated scenarios were done  
260 to understand how the system changed after the OWF construction. The BOWF model compared to the REEF  
261 scenario showed: 1) an increase in top predators activity (except for diving seabirds), elasmobranchs, Atlantic  
262 cod, whiting, pouting, European sprat, sea bream, flatfish, benthic invertebrate predators, filter feeders and  
263 bivalves; 2) a decrease in benthic invertebrate deposit feeders, suprabenthos and King Scallop (Fig. 2). The  
264 comparison between the BOWF model and the COMBINED scenario differed from the previous comparison  
265 for the following compartments: mackerel, sea bass and King Scallop which showed an increase in their  
266 activity (Fig. 2). Finally, the comparison between the BOWF model and the OPTIM scenario differed from the  
267 two previous comparisons as 1) the activity of the lower trophic levels (zooplankton, bacteria, suprabenthos)  
268 and some top predators (cetaceans, cephalopods) had increased, and 2) the activity of benthic invertebrate  
269 filter feeders, sea bream, sprat, pouting, and whiting decreased (Fig. 2).

270 <Figure: 2>

271 **3.2 MTL comparisons between scenarios**

272 A change in the food web structure was observed when simulating the “reef effect”. This applied to both the  
273 REEF and COMBINED scenarios that registered a decrease in the MTL compared to the BOWF and OPTIM  
274 situations (Fig. 4). Firstly, when considering the whole consumers’ community (i.e. MTL\_2.0), a decrease of  
275 0.1 in the MTL was noticed, which seemed to be driven by the important increase in the benthic bivalves’  
276 biomass (TL = 2.1). Bivalves doubled their biomass from around 19 gC.m<sup>-2</sup> in the BOWF and OPTIM scenarios  
277 to more than 40 gC.m<sup>-2</sup> in the REEF and COMBINED scenarios (Fig. 3). The important increase of bivalves’  
278 biomass went along with an increase in the biomass of the benthic filter feeders and a decrease in the

279 biomass of a higher TL functional group (i.e. European pilchard), which strengthened the decrease in the  
280 global MTL. Secondly, after excluding the low trophic level species (i.e. MTL\_3.25), the decrease in the MTL  
281 was even more marked (more than 0.3 decrease in MTL) between BOWF-OPTIM and REEF-COMBINED. This  
282 decrease was not influenced anymore by the bivalves' biomass change as this functional group was excluded.  
283 The main functional groups driving the MTL\_3.25 trend (i.e. functional groups representing 95% of the total  
284 biomass) were exclusively fish functional groups (Fig. 3). Within these functional groups, two of them showed  
285 a marked shift between BOWF-OPTIM and REEF-COMBINED. The pouting biomass doubled but, in the same  
286 time, its TL decreased (i.e. TL of pouting decreased from 3.7 in BOWF-OPTIM to 3.3 in REEF-COMBINED, see  
287 Table 2). The combination of a biomass increase and a TL decrease resulted in a decreasing trend of the  
288 MTL\_3.25. In this case, the change in the TL of pouting between scenarios highly influenced the MTL trend.  
289 Indeed, when applying a unique mean TL value for all scenarios (TL mean between the different scenario for  
290 each group), the decrease in MTL between BOWF-OPTIM and REEF-COMBINED was significantly reduced.  
291 The MTL decrease was also stressed by the important decrease in the relative biomass of piscivorous fish (TL  
292 = 3.8). Thirdly, when focusing on top predators (i.e. MTL\_4.0), the registered decrease in MTL trend was  
293 around 0.1, similar to the observed decrease in MTL\_2.0 (Fig. 3). The shark and rays functional group showed  
294 an important increase in its biomass while a decrease in the TL of this functional group was observed between  
295 BOWF-OPTIM and REEF-COMBINED (Table 2). Again, the combination between biomass increase and TL  
296 decrease has resulted in a decreasing trend of the MTL\_4.0. The MTL decreasing trend at the three cut-offs  
297 (i.e. MTL\_2.0, MTL\_3.25 and MTL\_4.0) was thus driven by an important restructuring of functional groups'  
298 biomass with the "reef effect" coupled to the modification of the functional groups' TL in relation to the  
299 simulated scenarios.

300 <Figure 3>

### 301 **3.3 ENA indices and ecosystem attributes comparisons between scenarios**

302 From a methodological perspective, the single ENA indices values derived from the EwE software for T., A,  
303 A/C, AMI, R, R/C were included in the distributions calculated by the ENAtool routine for the BOWF model  
304 and the three scenarios (Fig. 4). For the FCI index, the Ecopath point estimates were included in the  
305 distributions for the BOWF model and the OPTIM scenario and were above the upper boxplot whisker for  
306 the REEF and COMBINED scenarios.

307 <Figure 4>

308 No significant differences were observed between the BOWF model and the OPTIM scenario for all ENA  
309 indices (Fig 4; Table 3). In comparison, the T.. increased significantly between the BOWF and the REEF

310 scenario as well as between the REEF and the OPTIM scenario. R increased significantly between the BOWF  
311 model and the REEF scenario. A similar pattern was observed between the BOWF model and the COMBINED  
312 scenario as well as between the REEF and COMBINED scenarios. The ratio R/C increased significantly between  
313 the BOWF model and the COMBINED scenario as well as between the REEF and the COMBINED scenario. On  
314 the opposite, the AMI decreased significantly between the BOWF model and the COMBINED scenario as well  
315 as between the REEF and the COMBINED. Finally, no significant changes were noticed for the FCI index  
316 between the BOWF model and the three scenarios (Table 3).

317 <Table 3>

318 The graph of the transfer efficiencies (TE) as function of the trophic level showed a similar pattern between  
319 the BOWF model and the three scenarios, decreasing with increasing TL in all models (Fig. 5). Nonetheless,  
320 values were lower in the REEF and COMBINED scenarios compared to the two other situations.

321 <Figure 5>

322 Concerning the other ecosystem attributes, results showed that the total PP/R decreased between the BOWF  
323 model and both the REEF and COMBINED scenarios, by approximately 35% (Table 4). The B/T.. increased  
324 between the BOWF model and both the REEF and COMBINED scenarios, by approximately 33% (Table 4).

325 <Table 4>

## 326 **4. DISCUSSION**

### 327 **4.1 Methodological issues**

328 The Ecopath model of the Courseulles-sur-mer area was based on local, highly replicated, and detailed  
329 samplings (Raoux et al., 2017). The overall pedigree index (0.523) for this model fall into the upper range of  
330 pedigree values obtained for other published models, confirming the relatively low level of data uncertainty.  
331 Compared to what was done previously by Raoux et al. (2017), the moderate uncertainty around the input  
332 data were taken into account with the ENAtool routine when analysing the outputs of the model and  
333 scenarios (Guesnet et al., 2015). Thus, statistical comparisons between the BOWF model and the 3 scenarios  
334 was performed. It is worth noting that the ENAtool allows to calculate uncertainty only for the ENA indices.  
335 This methodology brought rather substantial differences to the conclusions. For instance, Raoux et al. (2017)  
336 found an increase of 40% of the FCI between the BOWF model and the REEF scenario. However, in the present  
337 paper, this difference appeared none significant. Nonetheless, from a methodological point of view, this

338 routine needs further development, particularly to reduce the computation time through parallel calculations  
339 for highly constrained models. In addition, allowing to quantify the uncertainty around the changes in the  
340 initial parameters such as compartment biomass and TL of the functional groups would be a useful addition  
341 to this method.

#### 342 **4.2 The MTL a good indicator to assess changes in trophic webs**

343 The MTL was first applied on fish landings' data by Pauly et al. (1998) which led to the famous concept of  
344 "fishing down the marine food webs". The rationale behind this indicator is that a decline in MTL values  
345 indicates a gradual transition in the food web from long-lived, high trophic level piscivorous fish, towards  
346 short-lived, low trophic levels such as invertebrates and planktivorous fish. The resulting shorter food chain  
347 reduces the food webs' complexity, increasing the systems' vulnerability to both natural and anthropogenic  
348 perturbations (CBD 2004, Pauly and Watson 2003). In the current study, the MTL was applied to describe the  
349 food-web structure under different scenarios after the implementation of an offshore wind farm. The MTL  
350 showed a decreasing trend between BOWF-OPTIM and REEF-COMBINED scenarios, for all tested cut-offs (i.e.  
351 MTL\_2.0, MTL\_3.25, MTL\_4.0). However, the observed decrease in MTL was not due to the disappearance  
352 or reduction of higher trophic levels. The different MTL indices along with the functional groups' biomass,  
353 allowed to detect a reconstruction of the food web caused by the simulated "reef effect" (REEF and  
354 COMBINED scenarios), which induced an increase in the total biomass of lower trophic levels mainly (benthic  
355 invertebrates' filter feeders and bivalves). In this new configuration, the "reef effect" cascaded up to the  
356 higher trophic levels feeding on filter feeders, which also increased in biomass. However, their increase in  
357 biomass is clearly overwhelmed by the large biomass increase in filter feeders, which resulted in a decrease  
358 in the relative biomass of higher trophic levels and a reduced MTL as a consequence.

359 The MTL indicator and the "fishing down marine food webs" concept has largely been tested and applied in  
360 the world oceans, generally on large ecosystem scales (Pinnegar et al., 2002; Ainley and Pauly, 2014; Gascuel  
361 et al., 2016) and in global comparative approaches (Pauly et al., 1998; Pauly and Palomares, 2005). The  
362 application of MTL indicator on smaller geographical scales, such as the OWF scale, and in relation to OWF  
363 installation rather than direct fishing pressure impact, is rather rare. However, in most studies using the MTL  
364 indicator, TL values applied to calculate the indicator are generally unique values extracted from global  
365 databases such as Fishbase or Sealifebase (Froese and Pauly, 2017; Palomares and Pauly, 2017). The  
366 evolution of species TL according to the different scenarios was applied on MTL indicator in the current study  
367 which induced an increased sensitivity of the MTL indicator to the structural changes occurring in the  
368 ecosystem. Indeed, when a unique mean TL value per species was applied for all scenarios instead of using  
369 the various TL estimated by models in the various scenarios, the decrease in MTL trend between BOWF-  
370 OPTIM and REEF-COMBINED was significantly reduced. The interpretation of changes in the MTL indicator

371 should thus be made considering the geographical scale that is applied, the main human pressure that is  
372 considered, and the accuracy of the TL estimates in regard to the potential spatial and temporal difference  
373 in TL. In the OSPAR context, the appropriate geographical scale for integrating the various indicators is a  
374 current issue under consideration (Elliott et al. 2017, Haraldsson et al. 2017). An indicator can be applied at  
375 different geographical scales from large OSPAR regions to local subregional areas (Haraldsson et al. 2017).  
376 Interpretation of the MTL at different spatial scales should be made with caution, as this study shows that a  
377 decreasing trend in this indicator cannot be automatically translated as “unsustainable” status, but closer  
378 evaluation of the underlying reason is needed, at least at the small OWF scale.

379 The importance of having regular and accurate trophic level estimations that reflect the changes occurring  
380 in the food web was also highlighted in the current work. This emphasizes the importance of surveying the  
381 evolution of TL estimation in order for the MTL to detect accurately the changes that occurs in the food web.  
382 This has been highlighted previously (Bourdaud et al., 2016, Arroyo et al., 2017), and should be especially  
383 applied when this indicator is to be used for assessing the marine environmental status under management  
384 context.

385 In Heymans et al. (2014), the MTL was applied on worldwide food-web models along with ENA indices. These  
386 authors observed that the reduced MTL values were related to reduce transfer efficiency (TE) and high  
387 Ascendency (A) reflecting an energy efficient transfer up the food chain, with low omnivory but a food web  
388 high organization which is in line with the present ENA results as detailed below.

#### 389 **4.3 Ecosystem maturity and resilience: interpreting ratios and ENA patterns**

390 According to Odum (1969), ecosystems evolve towards maturity in a process that involves structural changes  
391 that are orderly, directional and predictable. Odum stated that the PP/R ratio is a functional index of  
392 ecosystem maturity, and is expected to be higher than 1 in immature systems, and tends to 1 as a system  
393 matures. The estimated PP/R values of the BOWF model and the three scenarios exceeded 1, meaning that  
394 they have not yet reached a mature stage. However, the PP/R values for the scenario related to a “reef effect”  
395 (REEF and COMBINED) were lower (table 4), suggesting a more mature ecosystem under these scenarios.  
396 These results are in line with the high B/T.. values in the REEF and COMBINED scenarios, which in fact, are  
397 expected to increase as an ecosystem matures (Odum, 1971).

398 According to our model and scenarios thirty years after the implantation of the OWF, the reserve effect  
399 seems to have a relatively limited overall impact on the ecosystem. In fact, changes in the ENA indices  
400 between the BOWF model and the OPTIM scenario were not significant. This could be explained by the fact  
401 that the area which would be closed to the fisheries would be too small to have a significant impact at the  
402 ecosystem level. Meanwhile, significant changes were observed in the ENA indices between the BOWF model

403 and the different “reef effect” scenarios (REEF and COMBINED), which may have potential consequences in  
404 terms of resilience of the system. The term resilience can refer to two different aspects of system stability:  
405 engineering resilience and ecological resilience (Holling, 1996). The “engineering resilience” concept assumes  
406 the existence of a local equilibrium; a system with a short return time to equilibrium will be more resilient  
407 than one with a longer return time (Pimm, 1984; Holling, 1996). On the other hand, a system might exist in  
408 more than one stable state, a condition called “multiple stable states”. In this case, resilience would be  
409 defined as the measure of the pressure magnitude that can be absorbed before the system crosses a  
410 threshold and settles into another state. Holling (1996) called this second concept “ecological resilience”.  
411 Here, to interpret the differences in ENA indices between the BOWF model and the REEF/COMBINED  
412 scenarios, we will focus on ecological resilience as it is more applicable to changes observed by ecologists  
413 (Gunderson, 2009).

414 It has been demonstrated that resilience for a system is strongly related to its structure and functioning  
415 (Chapin et al., 1997). ENA indices are therefore powerful tools as they link system architecture to system  
416 function, revealing the emergent properties (Ulanowicz, 2004). ENA indices have been calculated in several  
417 marine and coastal ecosystems to assess their trophic structure (Rybarczyk et al., 2003). In fact, under  
418 stressful conditions, the emergent properties of an ecosystem can change (Mukherjeer et al., 2015; Tecchio  
419 et al., 2015; Pezy et al., 2017). Ascendency increased significantly in the REEF and COMBINED scenarios.  
420 According to Ulanowicz (1986), this index allows to assess the development status or maturity of an  
421 ecosystem. Ulanowicz et al. (1997) stated that high values of Ascendency represent a mature system whereas  
422 low values indicate a stressed or immature system (Ulanowicz, 1997; Ortiz and Wolff, 2002; Patricio et al.,  
423 2006; Baird et al., 2009). More specifically, during maturation, ecosystems develop in order to increase their  
424 activity (T..) and energy storage, and they tend towards greater Ascendency (Ulanowicz, 1997). The highest  
425 possible value of Ascendency is called the development capacity (C) which represents the real potential  
426 reached by the system in terms of structure. Our results indicated that the ecosystems under a “reef effect”  
427 (REEF and COMBINED), seems to be more mature than in the BOWF model and OPTIM scenarios, which  
428 agrees with the PP/R and B/T.. ratios. However, a high value of Ascendency also means the system is more  
429 active in constraining flows along more specific pathways, and so the system can lose flexibility which could  
430 lead to an ecosystem with less resilience. Although the Ascendency increased significantly in the “reef effect”  
431 scenarios (in the REEF and COMBINED scenarios), the significantly increased redundancy (R) suggest that the  
432 ecosystem did not lose its flexibility. The redundancy (or overhead), which is the difference between the  
433 internal capacity ( $C_i$ ) and the internal Ascendency ( $A_i$ ), is an indicator of the inefficiency of the network (the  
434 ecosystem part which is not organised). It measures the number of parallel trophic pathways connecting the  
435 different trophic compartments (Ulanowicz and Norden, 1990). The redundancy is based on the idea that  
436 within an ecosystem, some species can functionally replace others (McCann, 2000; Woodward, 2009). These

437 redundant species can be considered as “guarantors” resulting in a reliable ecosystem functioning (Naeem,  
438 1998). Thus redundancy increases the ecosystem resilience as this reservoir of energy acts as an insurance  
439 against perturbations (Naeem, 1998 ; Costanza, 1999). The significant increase in both Ascendency and  
440 redundancy indicate that after the installation of the OWF, the ecosystem keeps its balance (or equilibrium)  
441 between the organised (Ascendency) and non-organised part (redundancy or overhead), which will bring  
442 flexibility to potential perturbations as the energy transfers through the trophic network can be maintained  
443 via other pathways (Ulanowicz et al., 2009). In addition, according to Mukherjee et al. (2015), the ecosystem  
444 after the installation of a OWF seems to be in a healthy state as it “can develop an efficient diversity of  
445 components and exchange pathways (high organization) while maintaining some overhead (redundancy) or  
446 resilience as insurance against stress”.

447 Adding to this, the TE decreased with TL in the model and scenarios without any interruptions. This indicates  
448 that the compartments functionally behaved in a similar way before and after the OWF construction.  
449 According to Coll et al. (2009), important perturbations can be detected by analysing the TE profile. In fact,  
450 these authors showed that ecosystems undergoing a perturbation such as intense fishing activities, showed  
451 breaks in the typical decreasing pattern of TE. This observation of stable TE profiles strengthened our  
452 conclusion that the Courseulles-sur-mer OWF construction adds limited stress on the ecosystem. This result  
453 can be explained by the fact that the Bay of Seine is historically influenced by a high level of human activities  
454 (Dauvin, 2006) may have led to an increased resilience over time to face these multiple pressures (Pezy et  
455 al., 2017). However, it is worth noting that our model and simulated scenarios did not take into account all  
456 possible effects generated by potential changes in the community, as we chose to use estimates derived from  
457 the literature and expert knowledge, and not from complex models. For instance, our simulation did not take  
458 into account the potential arrival of invasive species. In fact, some authors suggest that OWF could act as  
459 stepping stones for invasive species (Wilhelmsson and Malm, 2008). One example, is the giant chironomid,  
460 *Telmatogeton japonicus*, that have been recorded in the intertidal zone of the wind turbines at Utgrunden,  
461 Baltic sea (Wilhelmsson and Malm, 2008).

462 To summarise, ENA indices bring together different holistic indices giving the currently most complete view  
463 of an ecosystem approach. They also show a high sensitivity to detect ecosystem changes under different  
464 conditions (Dame and Christian, 2007). However, the ecological interpretation remains sometimes complex,  
465 as establishing the link between ENA indices and system resilience or maturity (*sensu* Odum) is still in  
466 progress. Thus, the interpretation of their behaviour needs further definitions and contrasted case-studies  
467 before they can be useful to characterise ecosystem health and for management purposes.

## 468 **5 Conclusions**

469 An Ecopath model of the food web flows at the Courseulles-sur-mer OWF site was built allowing to 1)  
470 summarize all available ecological data on this site, 2) test different known impacts of OWF at the ecosystem  
471 level, 3) investigate the contribution of ENA indices in the assessment of ecosystem health state by  
472 confronting them to other indicators commonly-used by the scientific community, and 4) analyse the  
473 consequences of potential OWF impacts on ecosystem maturity and resilience through both ENA indices and  
474 other ecosystem attributes (Odum, 1969; 1971; Ulanowicz, 1986). Our results revealed a combination of  
475 changes in the ecosystem structure and functioning through the analysis of the ENA indices, MTL, and  
476 ecosystem attributes. After the installation of the OWF, the ecosystem is expected to be more mature  
477 (according to Odum 1969, 1971) while still in a healthy state (according to Mukherjee et al., 2015). Moreover,  
478 our study suggested that the small size of the fisheries restriction area would not have any important impact  
479 on the ecosystem structure and functioning.

480

481 Nonetheless, as marine ecosystems face many natural and anthropogenic perturbations, there is an urgent  
482 need to understand how multiple perturbations interact to influence each other and their consequences on  
483 ecosystem functioning and stability (Crowe and Frid, 2015; Raoux et al., 2018). Thus, a natural next step  
484 would be to develop a holistic view of cumulated impacts within the OWF (Raoux et al, 2018). A qualitative  
485 modelling approach (Puccia and Levins, 1986) could suggestively be developed to analyse the ecosystem  
486 structure and dynamics, and to take into account ecosystem components and processes that are difficult to  
487 measure. This approach could allow to highlight key linkages between the different ecological components  
488 and other human dimensions (Dambacher et al., 2015). Integrating cumulative impacts and human  
489 dimensions in models fits within the socio-ecosystem approach (Mazé et al., 2015), is part of the field of  
490 sustainability sciences dedicated to find concrete applications for coastal management.

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498

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707 **Figure legends**

708 **Figure 1.** Location of the Courseulles-sur-Mer future offshore wind farm (which corresponds to the Ecopath  
709 model BOWF) and benthic communities in the Bay of Seine, north-western France (modified from Baffreau  
710 et al., 2017).

711 **Figure 2:** Differences in compartment throughflows between the three EwE simulations (scenario REEF,  
712 OPTIM and COMBINED) and the BOWF model. Note that the y-axis scale was log-transformed, and that this  
713 percentage analysis did not consider the difference in absolute values between functional groups. Grey bars  
714 identified both functional groups for which the biomasses have been set to their accumulated maximum  
715 during the Ecosim 30-years simulations of 'reef effect' as well as the functional groups for which a decrease  
716 in fishing effort have been set during the Ecosim 30-years simulations 'reserve effect'. Black bars, on the  
717 contrary, represented groups for which variations in biomass were an output of the Ecosim simulation across  
718 30 years.

719 **Figure 3.** Mean Trophic Level (MTL) and biomass ( $\text{gC}\cdot\text{m}^{-2}$ ) of functional groups for the four Ecopath models  
720 (BOWF model and OPTIM, REEF and COMBINED scenarios). Three MTL are applied to each scenario (black  
721 lines) in order to capture (i) the whole consumers' community (MTL\_2.0) with a cut-off of functional groups  
722 with  $\text{TL} < 2$ ; (ii) a focus on higher trophic level species (MTL\_3.25) excluding functional groups with  $\text{TL} < 3.25$ ;  
723 and (iii) a focus on top predators (MTL\_4.0) excluding functional groups with  $\text{TL} < 4.0$ . The functional groups  
724 displayed are those who represent 95% of the total biomass for each cut-off. For interpretation of colours  
725 the reader is referred to the online version of the article.

726 **Figure 4.** Boxplots of ENA indices for the four Ecopath models (BOWF model and OPTIM, REEF and COMBINED  
727 scenarios) using the ENAtool routine, where the median of the distributions was represented by a bold line.  
728 Red dots corresponded to the single ENA indices values obtained from the pre-existing Ecopath model using  
729 the EwE software. As a validation rule, these single values were all equal to the ENA indices values calculated  
730 after the importation of the pre-existing Ecopath model to Matlab with no change on the input parameters.  
731 Significant differences ( $p\text{-value} < 0.05$ ) are indicated by letter a, b and c.

732 **Figure 5.** Transfer efficiencies (TE) by discrete trophic levels for the four Ecopath models (BOWF model and  
733 OPTIM, REEF and COMBINED scenarios).

734 **Table 1:** Percentages of change applied on input parameters for the pedigree routine in the four Ecopath  
735 models (BOWF model and OPTIM, REEF and COMBINED scenarios) in the ENAtool routine. Values  
736 corresponded to a percentage of variation around the initial values provided in Table 2. Inv.: invertebrates;  
737 B: biomass (gC.m<sup>-2</sup>); P/B: production to biomass ratio (year<sup>-1</sup>); Q/B: consumption to biomass ratio (year<sup>-1</sup>);  
738 DC: diet composition.

	<b>Compartments</b>	<b>B</b>	<b>P/B</b>	<b>Q/B</b>	<b>DC</b>
1	Bottlenose dolphins	0.3	0.5	0.5	0.1
2	Harbour porpoises	0.3	0.5	0.5	0.1
3	Harbour seals	0.3	0.5	0.5	0.1
4	Grey seals	0.3	0.5	0.5	0.1
5	Diving seabirds	0.1	0.5	0.5	0.3
6	Surface feeders seabirds	0.1	0.5	0.5	0.3
7	Benthopelagic cephalopods	0.1	0.5	0.5	0.1
8	Benthic cephalopods	0.1	0.5	0.5	0.3
9	Fish. mackerel	0	0.5	0.5	0.3
10	Fish. European seabass	0.1	0.5	0.5	0.3
11	Fish. sharks and rays	0.1	0.5	0.5	0.3
12	Fish. Atlantic cod	0.1	0.5	0.5	0.3
13	Fish. whiting	0.1	0.5	0.5	0.3
14	Fish. Atlantic horse mackerel	0	0.5	0.5	0.3
15	Fish. gurnard	0.1	0.5	0.5	0.3
16	Fish. pouting	0.1	0.5	0.5	0.3
17	Fish. poor cod	0.1	0.5	0.5	0.3
18	Fish. European pilchard	0	0.5	0.5	0.3
19	Fish. European sprat	0	0.5	0.5	0.3
20	Fish. piscivorous	0	0.5	0.5	0.3
21	Fish. planktivorous	0	0.5	0.5	0.3
22	Fish. benthos feeders	0	0.5	0.5	0.3
23	Fish. sea bream	0.1	0.5	0.5	0.3
24	Fish. sole	0	0.5	0.5	0.3
25	Fish. European plaice	0	0.5	0.5	0.3
26	Fish. other flatfish	0	0.5	0.5	0.3
27	Benthic inv. predators	0.1	0.5	0	0.3
28	Benthic inv. filter feeders	0	0.5	0	0.3
29	Benthic inv. Bivalves filter feeders	0.1	0.5	0	0.3
30	King scallop	0.1	0.5	0	0.6
31	Benthic inv. deposit feeders	0	0.5	0	0.3
32	Suprabenthos	0	0.5	0	0.6
33	Meiofauna	0	0.3	0	0.6
34	Zooplankton	0.5	0.3	0.6	0.6
35	Bacteria	0.5	0.3	0	0.6
36	Phytoplankton	0.5	0.3	0	0
37	Detritus	0.5	0	0	0

739

740 **Table 2:** Biomass values, trophic level (TL) and Ecotrophic Efficiencies (EE) for the four Ecopath models (i.e.  
741 BOWF model and OPTIM, REEF and COMBINED scenarios).

Compartments	Biomasses gC.m <sup>-2</sup>				TL				EE			
	BOWF	OPTIM	REEF	COMBINED	BOWF	OPTIM	REEF	COMBINED	BOWF	OPTIM	REEF	COMBINED
Bottlenose dolphins	1.87 × 10 <sup>-5</sup>	2.1 × 10 <sup>-5</sup>	8.44 × 10 <sup>-5</sup>	8.70 × 10 <sup>-5</sup>	4.76	4.77	4.76	4.72	0	0	0	0
Harbour porpoises	4.10 × 10 <sup>-4</sup>	4.22 × 10 <sup>-4</sup>	1.43 × 10 <sup>-3</sup>	1.49 × 10 <sup>-3</sup>	4.63	4.64	4.61	4.57	0	0	0	0
Harbour seals	6.73 × 10 <sup>-4</sup>	6.62 × 10 <sup>-4</sup>	1.89 × 10 <sup>-3</sup>	1.89 × 10 <sup>-3</sup>	4.63	4.62	4.63	4.63	0	0	0	0
Grey seals	2.68 × 10 <sup>-4</sup>	2.65 × 10 <sup>-4</sup>	8.73 × 10 <sup>-4</sup>	8.74 × 10 <sup>-4</sup>	4.83	4.83	4.66	4.66	0	0	0	0
Diving sea birds	1.50 × 10 <sup>-2</sup>	1.54 × 10 <sup>-2</sup>	9.80 × 10 <sup>-3</sup>	9.72 × 10 <sup>-3</sup>	3.98	3.97	3.93	3.94	0	0	0	0
Surface feeders seabirds	2.08 × 10 <sup>-3</sup>	2.14 × 10 <sup>-3</sup>	1.27 × 10 <sup>-2</sup>	1.27 × 10 <sup>-2</sup>	4.07	4.06	3.95	3.95	0	0	0	0
Benthopelagic cephalopods	1.36 × 10 <sup>-2</sup>	1.88 × 10 <sup>-2</sup>	1.70 × 10 <sup>-2</sup>	2.36 × 10 <sup>-2</sup>	4.07	4.13	4.14	4.17	0.43	0.43	0.63	0.44
Benthic cephalopods	6.22 × 10 <sup>-3</sup>	6.52 × 10 <sup>-3</sup>	7.65 × 10 <sup>-3</sup>	9.48 × 10 <sup>-3</sup>	3.92	3.91	3.87	3.89	0.92	0.91	0.95	0.91
Fish. mackerel	2.39 × 10 <sup>-1</sup>	2.73 × 10 <sup>-1</sup>	2.30 × 10 <sup>-1</sup>	2.61 × 10 <sup>-1</sup>	3.14	3.14	3.10	3.10	0.99	0.99	0.99	0.99
Fish. European seabass	1.86 × 10 <sup>-2</sup>	2.22 × 10 <sup>-2</sup>	1.63 × 10 <sup>-2</sup>	1.83 × 10 <sup>-2</sup>	3.75	3.75	3.63	3.63	0.43	0.32	0.44	0.39
Fish. sharks and rays	1.20 × 10 <sup>-1</sup>	1.22 × 10 <sup>-1</sup>	1.64 × 10 <sup>-1</sup>	1.76 × 10 <sup>-1</sup>	4.15	4.15	3.99	3.99	0.13	0.11	0.13	0.08
Fish. Atlantic cod	1.97 × 10 <sup>-2</sup>	1.95 × 10 <sup>-2</sup>	6.87 × 10 <sup>-2</sup>	6.87 × 10 <sup>-2</sup>	4.03	4.03	4.12	4.12	0.28	0.27	0.58	0.52
Fish. whiting	6.80 × 10 <sup>-3</sup>	6.15 × 10 <sup>-3</sup>	2.84 × 10 <sup>-2</sup>	2.84 × 10 <sup>-2</sup>	4.12	4.12	4.12	4.12	0.99	0.99	0.99	0.99
Fish. Atlantic horse mackerel	1.41 × 10 <sup>-1</sup>	1.30 × 10 <sup>-1</sup>	6.36 × 10 <sup>-2</sup>	5.99 × 10 <sup>-2</sup>	3.83	3.83	3.70	3.70	0.99	0.99	0.99	1.00
Fish. gurnard	6.30 × 10 <sup>-3</sup>	6.21 × 10 <sup>-3</sup>	8.69 × 10 <sup>-3</sup>	8.67 × 10 <sup>-3</sup>	3.46	3.46	3.58	3.59	0.00	0.00	0.00	0.00
Fish. pouting	1.66	1.64	3.85	3.85	3.76	3.76	3.31	3.30	0.04	0.04	0.10	0.10
Fish. poor cod	8.60 × 10 <sup>-3</sup>	8.55 × 10 <sup>-3</sup>	1.64 × 10 <sup>-3</sup>	1.55 × 10 <sup>-3</sup>	3.72	3.72	3.72	3.71	0.96	0.96	0.99	0.99
Fish. European pilchard	4.76	4.73	3.68	3.65	2.80	2.80	2.79	2.79	0.99	0.99	0.99	1.00
Fish. European sprat	1.08 × 10 <sup>-1</sup>	1.04 × 10 <sup>-1</sup>	1.28 × 10 <sup>-1</sup>	1.30 × 10 <sup>-1</sup>	3.00	3.00	3.00	3.00	0.99	0.99	0.99	0.99
Fish. piscivorous	2.42 × 10 <sup>-1</sup>	2.37 × 10 <sup>-1</sup>	4.86 × 10 <sup>-3</sup>	3.36 × 10 <sup>-3</sup>	3.84	3.84	3.82	3.82	0.99	0.99	0.99	0.99
Fish. planktivorous	8.19 × 10 <sup>-1</sup>	8.13 × 10 <sup>-1</sup>	7.22 × 10 <sup>-1</sup>	7.16 × 10 <sup>-1</sup>	3.01	3.01	3.00	3.00	0.99	0.99	0.99	0.99
Fish. benthos feeders	1.21	1.20	2.50	2.50	3.76	3.76	3.55	3.55	0.99	0.99	0.99	0.99
Fish. sea bream	2.98 × 10 <sup>-2</sup>	2.99 × 10 <sup>-2</sup>	8.33 × 10 <sup>-2</sup>	8.61 × 10 <sup>-2</sup>	3.17	3.17	3.14	3.14	0.30	0.29	0.32	0.29
Fish. sole	5.07 × 10 <sup>-2</sup>	1.04 × 10 <sup>-1</sup>	9.80 × 10 <sup>-2</sup>	9.80 × 10 <sup>-2</sup>	3.44	3.44	3.35	3.35	0.99	0.97	1.00	0.97
Fish. European plaice	2.16 × 10 <sup>-2</sup>	4.53 × 10 <sup>-2</sup>	5.33 × 10 <sup>-2</sup>	1.24 × 10 <sup>-1</sup>	3.37	3.37	3.22	3.22	0.99	0.97	0.99	0.97
Fish. other flatfish	6.18 × 10 <sup>-3</sup>	7.55 × 10 <sup>-3</sup>	2.70 × 10 <sup>-2</sup>	2.70 × 10 <sup>-2</sup>	3.35	3.35	3.26	3.26	0.99	0.99	0.99	0.97
Benthic inv. predators	2.94	2.92	3.01	3.01	3.07	3.07	2.82	2.83	0.98	0.98	0.99	0.99
Benthic inv. filter feeders	3.12	3.13	4.78	4.78	2.21	2.21	2.21	2.22	0.99	0.99	0.99	0.99
Benthic inv. Bivalves filter feeders	19.50	19.4	42.90	42.90	2.10	2.10	2.10	2.11	0.01	0.01	0.01	0.01
King scallop	7.70 × 10 <sup>-1</sup>	1.09	7.43 × 10 <sup>-1</sup>	1.09	2.10	2.10	2.04	2.11	0.58	0.37	0.59	0.39
Benthic inv. deposit feeders	3.57	3.54	2.98	2.90	2.21	2.21	2.21	2.21	0.99	0.99	0.99	0.99
Suprabenthos	2.00	2.00	1.71	1.70	2.53	2.53	2.36	2.34	0.99	0.99	0.99	0.99
Meiofauna	9.70 × 10 <sup>-1</sup>	9.70 × 10 <sup>-1</sup>	1.06	1.06	2.10	2.10	2.10	2.10	0.99	0.99	0.99	0.99
Zooplankton	1.72	1.71	1.79	1.79	2.00	2.00	2.00	2.00	0.88	0.88	0.99	1.00
Bacteria	7.50 × 10 <sup>-1</sup>	7.48 × 10 <sup>-1</sup>	7.70 × 10 <sup>-1</sup>	7.70 × 10 <sup>-1</sup>	2.00	2.00	2.00	2.00	0.22	0.22	0.25	0.24
Phytoplankton	3.24	3.24	3.24	3.24	1.00	1.00	1.00	1.00	0.76	0.76	0.99	0.99
Detritus	19.00	19.00	19.00	19.00	1.00	1.00	1.00	1.00	0.49	0.49	0.8	0.83

742

743 **Table 3:** Significance level between scenarios for ENA indices using the maximum-statistic method for  
 744 multiple comparisons (AMI: Average Mutual Information; R/C: relative redundancy; A: ascendency; A/C:  
 745 relative Ascendency; R: redundancy; FCI: Finn’s Cycling Index; T..: Total system Throughput). Significant  
 746 differences (p-value < 0.05) are indicated in bold.

	AMI	R/C	A	A/C	R	FCI	T..
<b>BOWF / OPTIM</b>	0.696	0.430	1.000	0.971	0.920	1.000	0.997
<b>BOWF / REEF</b>	0.947	0.995	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.999	<b>0.001</b>
<b>BOWF / COMBINED</b>	<b>0.018</b>	<b>0.001</b>	<b>0.041</b>	<b>0.000</b>	<b>0.000</b>	1.000	0.530
<b>OPTIM / REEF</b>	0.112	0.742	<b>0.001</b>	<b>0.002</b>	<b>0.000</b>	0.986	<b>0.017</b>
<b>OPTIM / COMBINED</b>	0.055	0.075	<b>0.026</b>	<b>0.000</b>	<b>0.000</b>	1.000	0.567
<b>REEF / COMBINED</b>	<b>0.003</b>	<b>0.001</b>	0.636	<b>0.001</b>	<b>0.004</b>	1.000	0.864

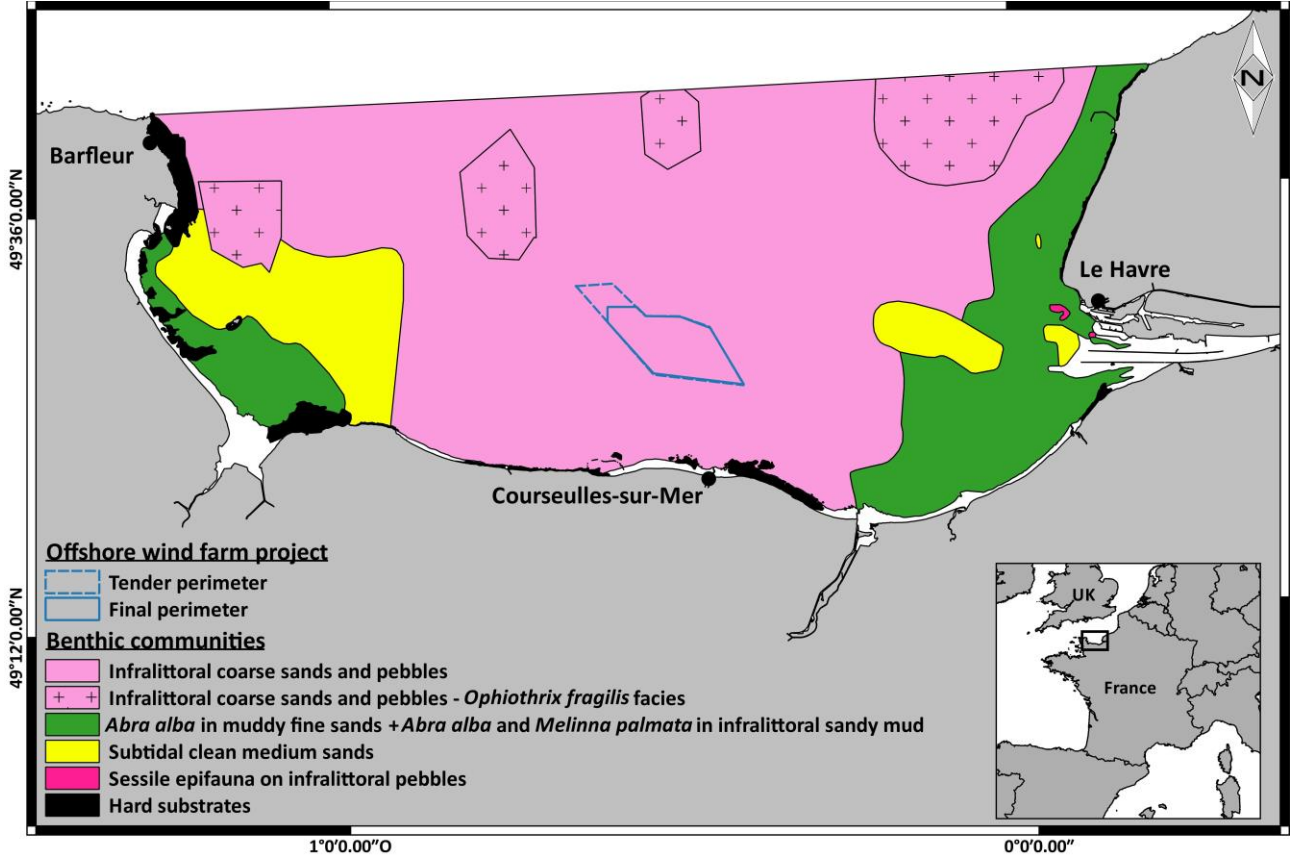
747  
 748

749 **Table 4:** Ecosystem attributes (PP/R: total primary production/total system respiration; B/T...: Total  
750 Biomass/ Total System Throughputs)  
751

Model and scenarios	PP/R	B/T.. (year)
BOWF model	1.72	0.03
OPTIM scenario	1.72	0.03
REEF scenario	1.12	0.04
COMBINED scenario	1.12	0.04

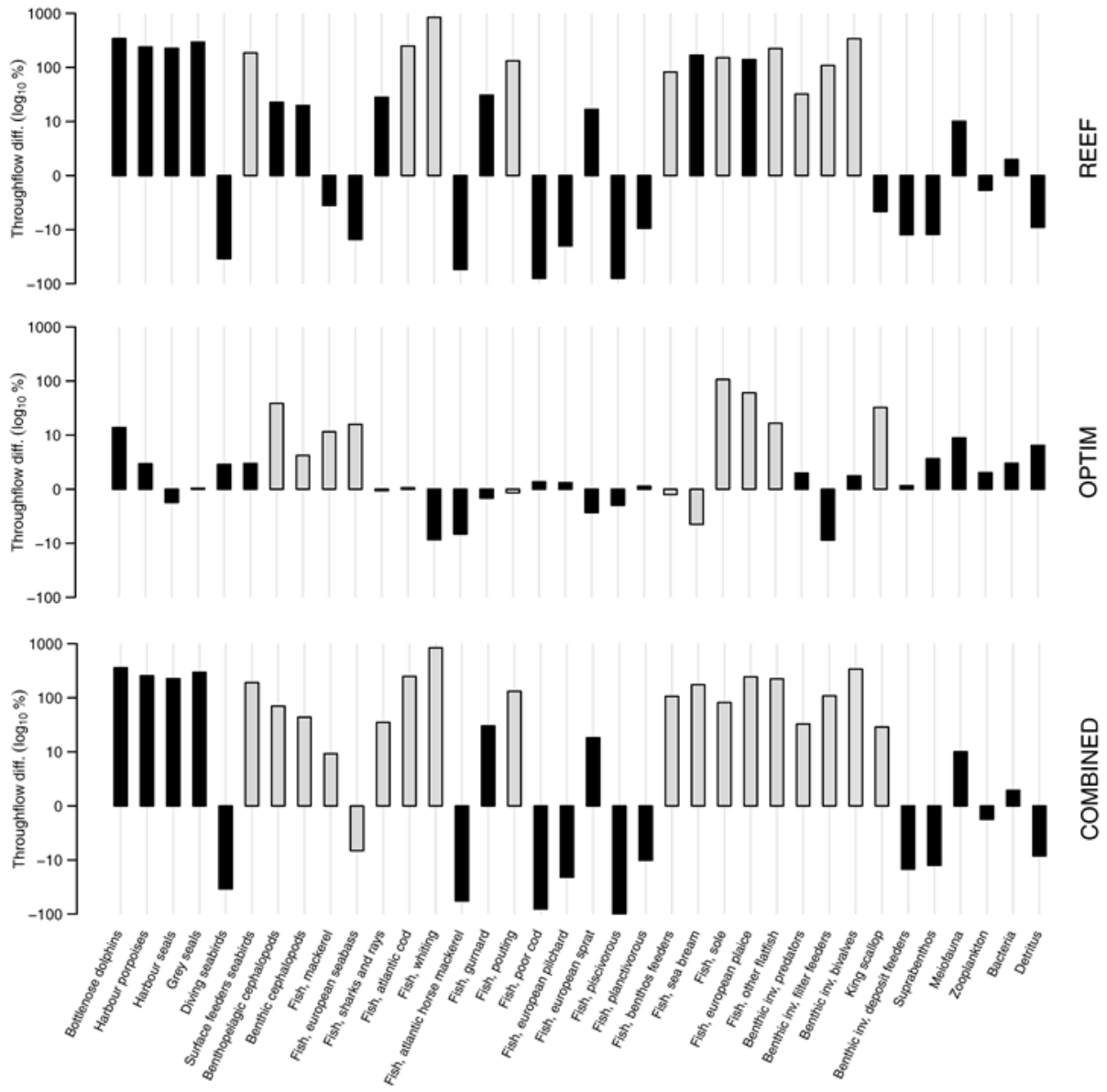
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754 **Figure 1.**



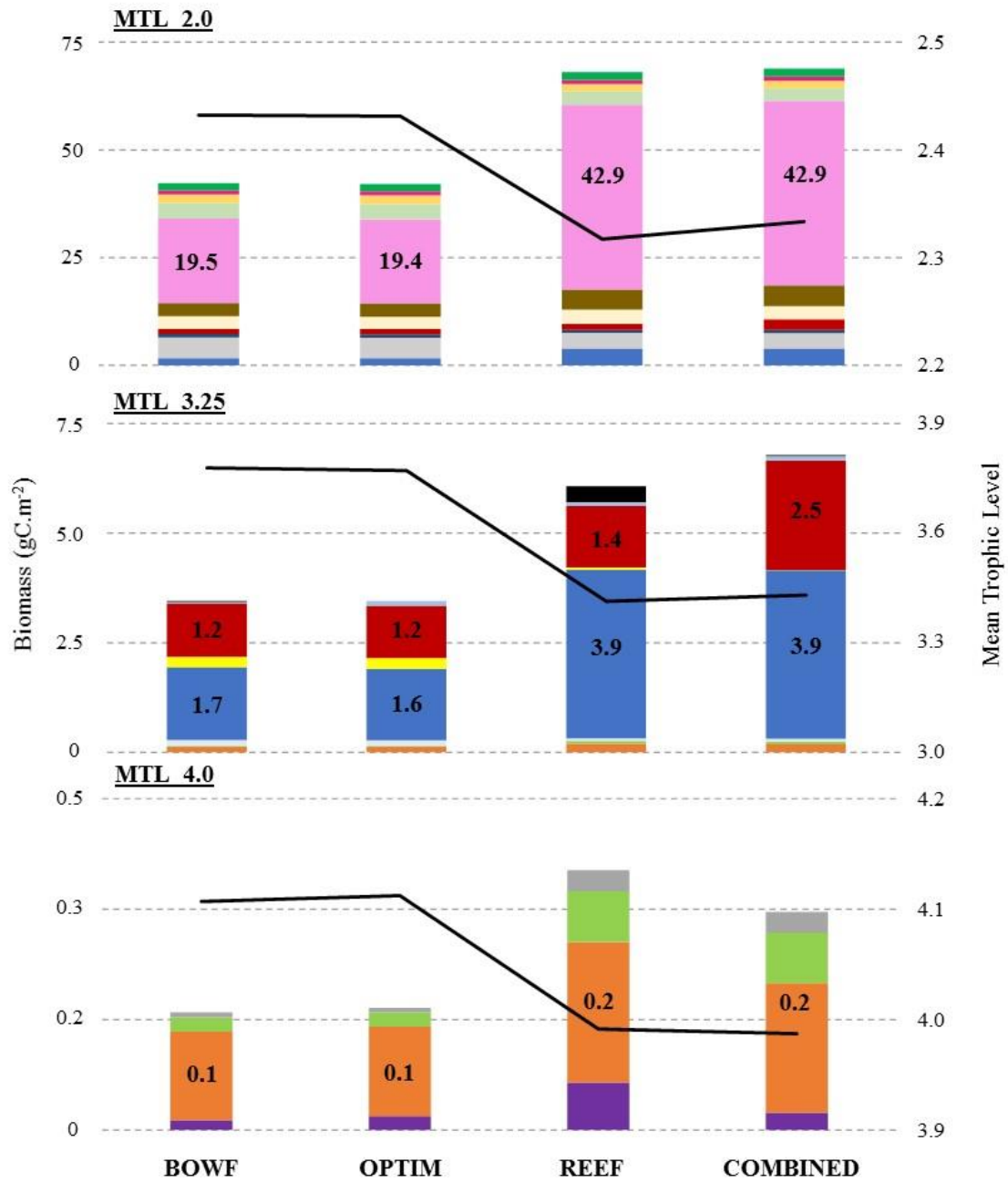
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757 **Figure 2.**



758  
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760 **Figure 3.**



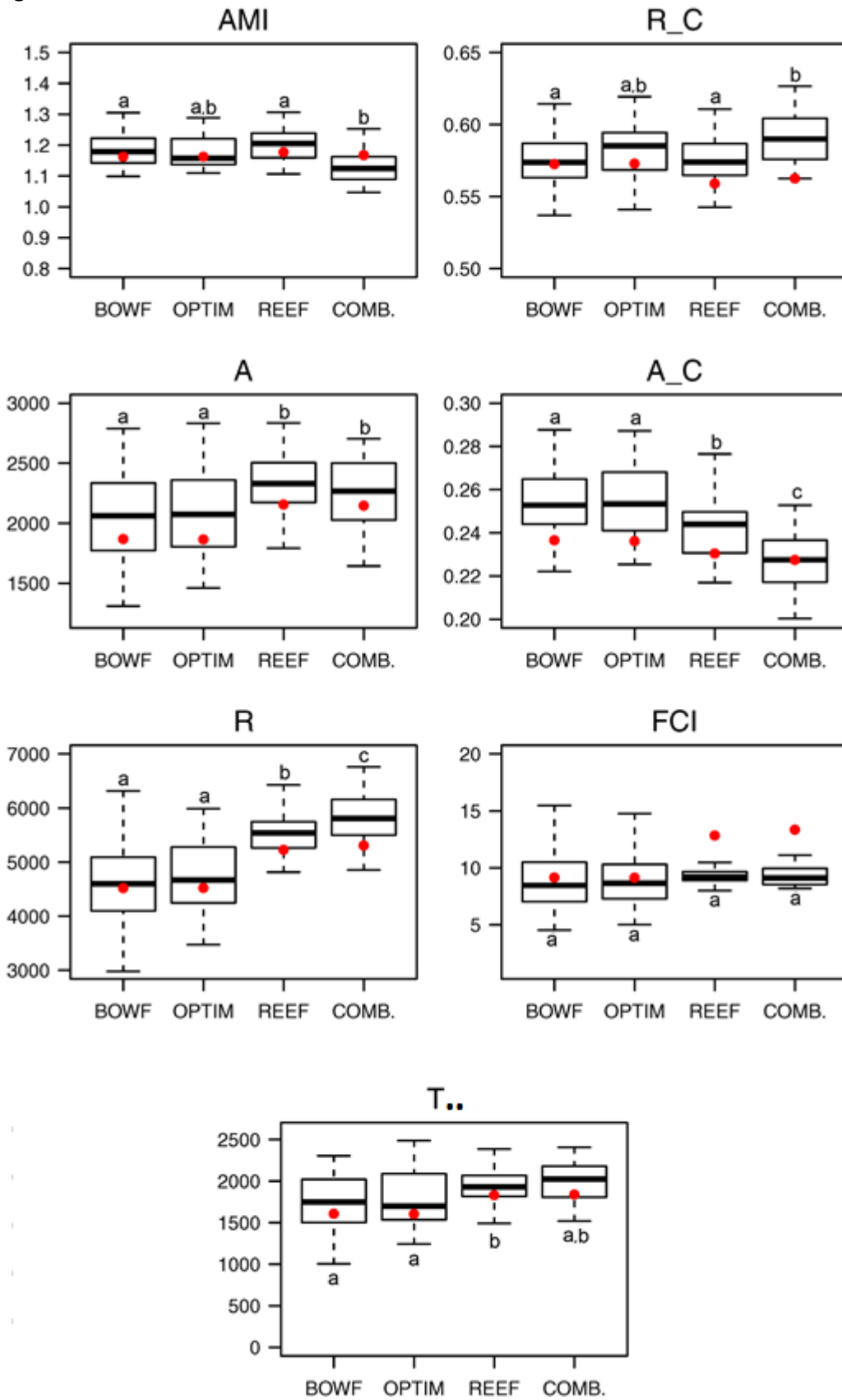
**Functional groups**

*Representing 95% of total biomass in each cut-off*



761  
762

763 **Figure 4.**

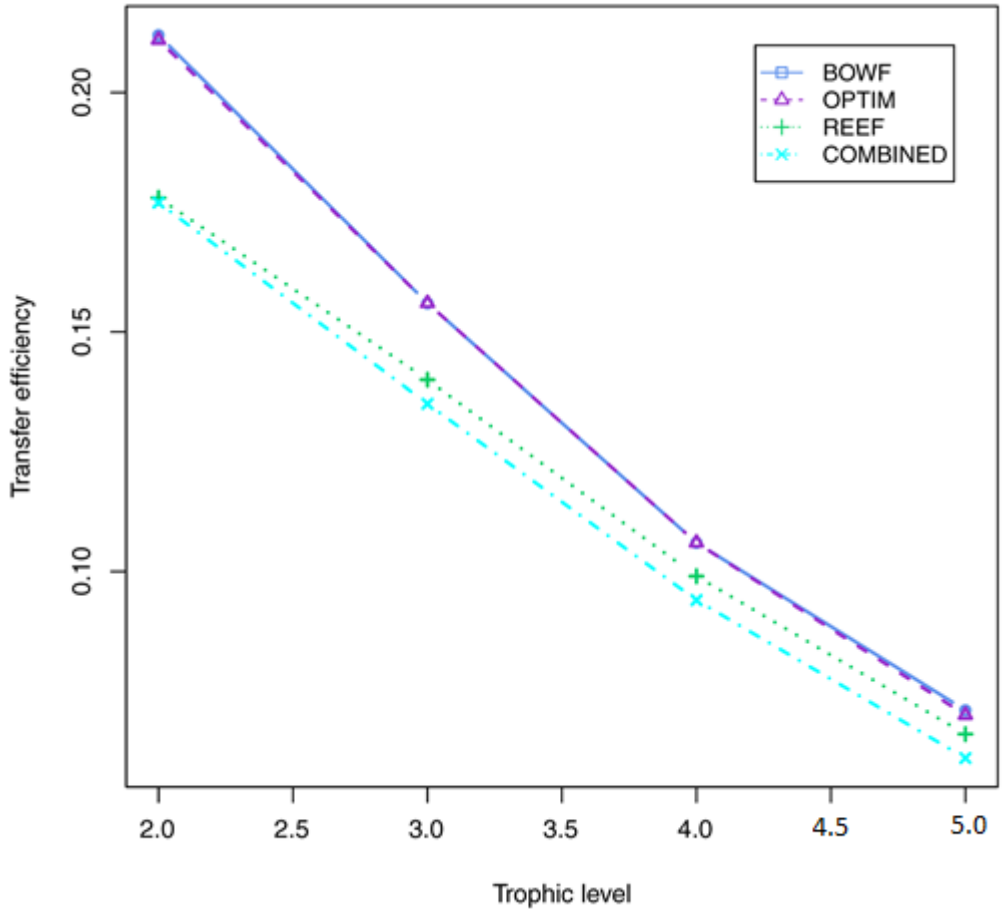


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767 **Figure 5.**



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