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Biomass of slow life history species increases as local bottom trawl effort decreases in the Celtic sea

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1 Abstract

2 Due to its selective removal, fishing pressure has long influenced the dynamics of
3 species based on their life history traits. Sensitivity to fishing increases along a “fast-
4 to-slow” gradient of life history strategies, and the “slow” species (large, long-lived,
5 late-maturing, giving birth to few large offspring) require the most time to recover from
6 fishing. In the North East Atlantic, after having reached extreme levels, fishing
7 pressure has decreased since the 1980’s due to management measures such as
8 total allowable catch (TAC) or area closure. An effect on the distribution of species as
9 well as a potential recovery could be expected. However, temporal patterns of life
10 history strategies are rarely linked to management measures. In addition, a larger
11 emphasis is often put on exploited or emblematic sensitive species but rarely on
12 assembly processes at the ecosystem scale (both commercial and non-commercial
13 species). Based on a 17-year time series of 101 taxa (fishes, elasmobranchs,
14 bivalves, cephalopods and crustaceans), we observed a negative relationship
15 between the biomass of taxa sensitive to fishing and bottom trawling pressure, as
16 well as an increase in their total biomass in the Celtic Sea. Over the whole area,
17 stochasticity appeared as the dominant assembly process. Deterministic assembly
18 processes were at play in the centre of the area where significant overdispersion
19 (caused by the presence of both slow and fast taxa) were observed. The absence of
20 sensitive taxa from the rest of the Celtic Sea appeared to be caused mainly by an
21 historical effect of environmental filtering when fishing was high. At the local scale,
22 we related the decrease in fishing pressure to the increase in biomass of five of the
23 most sensitive taxa. This local decrease in fishing pressure, resulting from the
24 implementation of an area closure, highlights the positive effect of such management
25 measures in less than two decades.

26

27 Keywords

28 Community weighted mean; Assembly processes; Biological traits; Elasmobranchs;

29 Area closure

30

31 1. Introduction

32 Marine ecosystems experience multiple pressures, the most severe of which
33 include climate change and fishing (Halpern et al., 2015). Climate change already
34 affects the structure, functioning and adaptive capacity of ecosystems by modifying
35 pH, temperature, oxygen concentration and food availability (Henson et al., 2017),
36 which notably results in displacement of species toward higher latitudes and deeper
37 waters (Cheung et al., 2013; Jorda et al., 2020). Its effects occur along with those of
38 fishing (Rogers et al., 2019), which has caused a decrease in biomass and even local
39 extinctions of species worldwide (Worm et al., 2006). It is widely acknowledged that a
40 population's ability to recover from disturbance depends on its demographic
41 dynamics, which are related to life history strategies (Le Quesne and Jennings, 2012;
42 Wiedmann et al., 2014).

43 Historically, life history strategies were characterised by their position along
44 the continuum of r strategies (energy allocated to producing many offspring) vs. K
45 strategies (energy allocated to producing a few extremely fit offspring) (Pianka,
46 1970). More recently, life history strategies of fish were described as a triangle: (i) an
47 opportunistic strategy for small, short-lived and rapidly maturing fish; (ii) a periodic
48 strategy for large, long-lived and highly fecund fish and (iii) an equilibrium strategy for
49 intermediate-sized fish that produce a few large offspring for which they provide

50 parental care (Pecuchet et al., 2018; Winemiller and Rose, 1992). These life history
51 strategies can be summarised along a fast-slow continuum (Beukhof et al., 2019b;
52 Juan-Jorda et al., 2013; Promislow and Harvey, 1990; Rochet et al., 2000) that
53 balances percentage of mortality and optimal size. Large and long-lived species that
54 mature late and give birth to large offspring lie at the “slow” end of the continuum
55 (Wiedmann et al., 2014). These species escape predation and have low natural
56 mortality rate, while the fast end is characterised by the opposite properties. Species
57 with a slow life history strategy are thus particularly sensitive to additional mortality,
58 such as that caused by anthropogenic pressures (e.g. fishing) (Brown et al., 2004;
59 Juan-Jorda et al., 2015; Kozłowski, 2006; Promislow and Harvey, 1990).
60 Understanding the spatio-temporal distribution of these slow life history species is
61 thus particularly useful for ecosystem management (Le Quesne and Jennings, 2012).

62 Identifying and explaining how species are distributed has long been a core
63 challenge in ecology. Evolutionary history, environmental variables and species
64 interactions drive the spatio-temporal distribution of species (Mouchet et al., 2013;
65 Webb et al., 2002). However, the distribution of the taxa could also arise from
66 random processes and the question of the relative importance of deterministic *versus*
67 stochastic assembly rules remains central (Vellend et al., 2014). Three major non-
68 exclusive assembly rules explain biodiversity patterns (Kraft et al., 2007):
69 stochasticity (Hubbell, 2001) and deterministic processes, namely environmental
70 filtering (Keddy, 1992; Zobel, 1997) and competitive exclusion (Hardin, 1960).
71 Environmental filtering implies strong abiotic control, which results in the survival of
72 species that have a narrow range of traits that enable them to endure environmental
73 pressures. The principle of competitive exclusion assumes that species can coexist if
74 they have different niche-related biological traits (Hardin, 1960). Thus, traits of

75 species in an assemblage may be similar if they are selected via environmental
76 filtering or different if they are selected via competitive exclusion. A careful
77 interpretation is essential and should be based on the biological understanding of the
78 processes at play. Indeed, competition (and more generally biotic interactions) can
79 lead to the same patterns as those driven by environmental filtering (Cadotte and
80 Tucker, 2017; Kraft et al., 2015) and community patterns result in both processes
81 interacting dynamically (Callaway et al., 2002; Kraft et al., 2015). Conversely to these
82 two deterministic assembly rules, neutral theory hypothesises that species coexist
83 regardless of their biological traits due to individual demographic stochastic events of
84 dispersal, birth and death (Hubbell, 2001; Vellend et al., 2014). The relative
85 dominance of stochastic and deterministic processes can be disentangled notably by
86 the comparison of the observed pattern with a null model (Vellend et al., 2014). The
87 prevalence of one assembly rule over the others could depends on the scale
88 considered. At the local scale, stochastic, biotic and abiotic parameters can act on
89 species simultaneously, and determining their relative importance remains
90 challenging (Mouillot et al., 2007). At larger scale, environmental filtering was
91 considered as having a larger effect than the other processes (Freschet et al., 2011).

92 Assembly processes in exploited marine ecosystems have attracted attention
93 only recently (Dencker et al., 2017; Ford and Roberts, 2020; Pecuchet et al., 2016),
94 as studies have historically focussed on freshwater and estuarine communities
95 (Mouillot et al., 2007; Peres-Neto, 2004; Schmera et al., 2013). Nevertheless the
96 understanding of the processes responsible for the structuration of exploited marine
97 communities can provide valuable inputs for their sustainable management (Dencker
98 et al., 2017). The North East Atlantic fishing grounds have shown signs of over-
99 exploitation since the 1970s (Gascuel et al., 2016), which caused species distribution

100 to be driven by fishing in addition to environmental and habitat characteristics, such
101 as temperature, depth and sediment (Foveau et al., 2017). We hypothesise that
102 gradual enforcement of European Union (EU) fishing policies over the past 40 years
103 that has decreased fishing pressure in the North East Atlantic (Fernandes and Cook,
104 2013) may have helped the biomass of species with slow life history strategies to
105 increase, reducing the strength of the environmental filter imposed by fishing on taxa.
106 However, temporal patterns of life history strategies of commercial and non-
107 commercial taxa are rarely studied as a function of environmental or anthropogenic
108 variables, and should be taken into account in management measures more
109 frequently (Fromentin and Fonteneau, 2001; Matson and Gertseva, 2020).

110 The Celtic Sea has been extensively fished for decades with a peak of the
111 number of species significantly exploited in the 1990's (Gascuel et al., 2016;
112 Guénette and Gascuel, 2012). Fishing thus likely imposed a major filtering on the
113 distribution of the taxa. Fishing mortality has then decreased at the ecosystem scale
114 since 2010 (Moullec et al., 2017) with the implementation of more restrictive TAC and
115 the creation of a closure area in the North of the Celtic Sea (ICES, 2007).
116 Environmental variables in the Celtic Sea were relatively stable over the recent
117 period (2000-2016). Since a clear impact of climate change, such as an increase in
118 bottom temperature, is not visible yet (Mérillet et al., 2020), the decrease in fishing
119 effort most likely had the largest influence on the recent distribution of life history
120 strategies in the Celtic Sea. Based on a 17-year time series, we explore the influence
121 of fishing on the spatio-temporal distribution of life history strategies in the benthic-
122 demersal community by considering 101 commercial and non-commercial taxa. We
123 assessed (i) which assembly processes and (ii) which environmental and
124 anthropogenic variables drive the spatio-temporal distribution of sensitivity to fishing.

125 Finally, (iii) we focussed on the trend of the biomass of sensitive taxa and bottom
126 trawl fishing at the local scale.

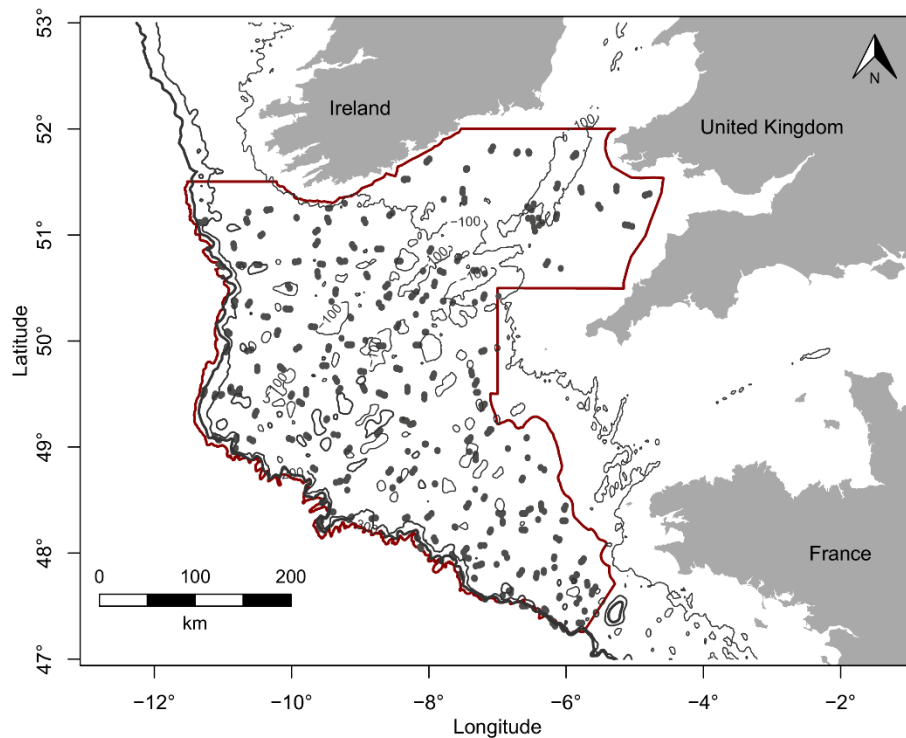
127

128 2. Material and methods

129 2.1. Taxa biomass and life history traits

130 For the 2000-2016 period, data on species biomass were extracted from the
131 EVHOE (*Evaluation des ressources Halieutiques de l'Ouest de l'Europe*) surveys, an
132 International Bottom Trawl Survey (ICES, 2015) performed every November in the
133 Celtic Sea. These surveys provide reliable and consistent data for evaluating the
134 impact of fishing as they are independent from fishing effort and follow the same
135 standardised protocol each year. EVHOE surveys use a 36/47 GOV (*Grande*
136 *Ouverture Verticale*) net fitted with a 20 mm cod end mesh, with a horizontal opening
137 of ca. 20 m and a vertical opening of 4 m. Sampling hauls are performed at 4 knots
138 for 30 min and follow a random stratified design based on sediment-depth strata
139 within a bank of possible hauls. They are not at the same location from one year to
140 another, but due to random sampling a same haul can be visited several times
141 across the time series. From 2000-2016, the surveys performed 53-84 valid hauls per
142 year, for a total of 1175 hauls. Due to variations in the accuracy of species
143 identification, some species were grouped into higher taxonomic levels (hereafter,
144 'taxon'; genus, for species of *Alloteuthis*, *Argentina*, *Arnoglossus*, *Gaidrosparus*,
145 *Loligo*, *Munida*, *Mustelus*, *Octopus*, *Pomatoschistus* and *Sepiola*; family, for
146 Ammodytidae and Gobiidae). To identify temporal changes in taxa biomass, only
147 those taxa that occurred at more than 5% of the sampling sites in at least one
148 EVHOE depth strata over the time series were kept for analysis and considered
149 correctly sampled. This process identified a total of 101 taxa from six classes

150 (Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii, Holocephali and
151 Malacostraca). Biomass was standardised by the area sampled during each haul and
152 then log-transformed to reduce variability. Sampling sites were located at depths of
153 57-340 m (Fig. 1), mainly on sand, mud, mixed sediments, coarse sediments and
154 boulders (Fig S1).



155

156 *Figure 1. Map of sampling sites (grey dots) in the study area in the Celtic Sea. The red line delineates the limits of*
157 *the study area, as defined in the EVHOE surveys.*

158

159 We selected the following biological traits for their known response to fishing
160 pressure: maximum length, longevity, age at maturity, offspring size, reproductive
161 guild and fecundity (Barlow, 1981; Brown et al., 2004; Jennings and Kaiser, 1998;
162 Jeschke and Kokko, 2009; Le Quesne and Jennings, 2012; Pecuchet et al., 2016;
163 Shephard et al., 2012; Tillin et al., 2006; Tyler-Walters et al., 2009; Wiedmann et al.,

164 2014) (Table 1). Values of these traits were extracted from the literature and the
 165 PANGAEA data library (Beukhof et al., 2019a) (see Table S1 for more details).

166 *Table 1: Life history traits used and their relevance, when used all together, to characterise life history*
 167 *strategy and sensitivity to fishing.*

Traits	Description	Relevance
Maximum length	in cm	Relates to many characteristics of an organism (Brown et al., 2004). Fishing is known to have led to the decrease in abundance of large body size taxa (Shephard et al., 2012)
Longevity	in year (maximum reported age)	Fishing is known to have led to the decrease in abundance of long-lived taxa (Shephard et al., 2012; Tillin et al., 2006)
Offspring size	in mm; Diameter of the released eggs, length of the egg case or length of the young for the bearer taxa	Informs on the parental investment and the energy needed for the production of one offspring (Winkler and Wallin, 1987). Perturbations, and thus fishing, select for taxa with small offspring (Jeschke and Kokko, 2009; Wiedmann et al., 2014). Linked to the resilience of the taxa after fishing event.
Age at maturity	in year	Informs on generation time (Pecuchet et al., 2016; Tillin et al., 2006). Fishing favors early maturing taxa (Claireaux et al., 2018; Shephard et al., 2012). Linked to the resilience of the taxa after fishing event.
Reproductive guild	Bearer - giving birth to a free living progeny. Guarder - eggs protected (carried under the abdomen for crustaceans) or guarded. Non guarder - pelagic eggs.	Informs on the parental investment and the energy needed for the production of one offspring (Barlow, 1981; Tillin et al., 2006). Linked to the resilience of the taxa after fishing event.
Fecundity	Segment of offspring number per female 1-1000: low 1000-100,000: medium 100,000-1,000,000: high >1,000,000: very high	Capacity of the population to recover; productivity of the taxa (Pecuchet et al., 2016). Fishing depleted low fecundity taxa (Shephard et al., 2012). Linked to the resilience of the taxa after fishing event.

168

169 We used Hill-Smith analysis (Hill and Smith, 1976), which is a principal
 170 component analysis that considers both quantitative and qualitative variables, to
 171 assess the sensitivity of each taxon based on the six life history traits selected. The
 172 first axis of the Hill-Smith analysis explained the most variability in the distribution of

173 life history traits across taxa. It was used as a sensitivity score (the more positive the
174 score, the more sensitive the taxa are) and also reflects the life history strategy of the
175 taxon.

176

177 2.2. Community assembly processes

178 To identify community assembly processes related to life history traits over the
179 2000-2016 period, we calculated the community-weighted variance (CWV) according
180 to Gaüzère et al., (2019) for the sensitivity score (and each of the six life history traits,
181 see Fig. S2). Assembly rules were assessed using a standard effect size (SES) by
182 comparing the CWV to a null model based on random community assembly (i.e.
183 1000 random permutations of trait values among taxa) (Gotelli and McCabe, 2002).
184 The null model consists in shuffling the traits of occurring taxa at each site so that
185 taxa richness remains constant at each site. If the observed CWV was not
186 significantly different from the random CWV, stochasticity was at play. Significant
187 deviation of the CWV from the random mean CWV and negative SES values
188 indicated underdispersion, meaning that the observed trait variability was lower than
189 expected by chance. Conversely, significant deviation and positive SES values
190 indicated overdispersion and an observed trait variability higher than expected by
191 chance.

192 The SES was calculated for each sampling site over the 2000-2016 period as (1).

$$193 \quad SES_i = \frac{x_{obs,i} - x_{th,i}}{SD_{th,i}} \quad (1)$$

194 with $x_{obs,i}$ the observed CWV at site i , $x_{th,i}$ the mean of the theoretical values
195 simulated by the null models at site i (hereafter referred as “mean random CWV”) and

196 $SD_{th,i}$ the standard deviation of these theoretical values simulated by the null models
197 at site i .

198 The significance of the deviation of the observed CWV from the random mean CWV
199 was calculated with a permutation test, performed with the *krandtest* function of the
200 “ade4” R package (Thioulouse et al., 2018). P-values of these tests were adjusted for
201 multiple testing (Benjamini and Yekutieli, 2001). Inverse-distance-weighting
202 interpolation was used only for graphical representation.

203

204 2.3. Life history trait distribution as a function of environmental and fishing 205 variables

206 To relate the spatio-temporal distribution of the sensitivity score and the life
207 history traits to environmental and fishing variables over 2000-2016 at the scale of
208 the Celtic Sea, community-weighted means (CWM) were calculated using the “FD”
209 package (Laliberté et al., 2014) for a community of R taxa as followed.

$$CWM = \sum_{i=1}^R p_i t_i$$

210

211 with p_i the $\log(x+1)$ transformed biomass of taxon i , and t_i the value of the sensitivity
212 score of taxon i (or each life history trait, see Fig. S3). The CWM of the sensitivity
213 score was modelled with a Gaussian distribution, so it was first transformed to make
214 it positive before applying the log function, ie the CWM of the sensitivity score was
215 $\log(x+c+1)$ -transformed, with $c=-\min(x)$ to get a positive or null variable. Like for
216 CWV, inverse-distance-weighting interpolation was used only for graphical
217 representation.

218 We selected environmental and fishing variables known to influence Celtic
219 Sea ecosystems, and more generally North Atlantic shelf ecosystems (Foveau et al.,
220 2017; Mérillet et al., 2020). Depth was recorded at each sampling site. Sediment data
221 according to Folk's 5-level classification system came from the EMODnet Geology
222 Portal (<https://www.emodnet-geology.eu>). Data for the few (95) sampling sites that
223 were not included in the EMODnet dataset were extrapolated from the SHOM
224 database (<https://diffusion.shom.fr/loisirs/sedim-mondiale.html>). As our community
225 data were based on annual sampling, and the 101 taxa studied display a wide variety
226 of life cycles, we assumed that annual means would be the most relevant values for
227 the covariables. Bottom temperature data were downloaded from Copernicus
228 (<http://marine.copernicus.eu>), from the Atlantic-Iberian Biscay Irish-Ocean Physics
229 Reanalysis data product at 8 km × 8 km resolution, while chlorophyll a data were
230 extracted from satellite observations at 1 km × 1 km resolution. Fishing effort data
231 were derived from the New Fisheries Dependent Information from the EU's Scientific,
232 Technical and Economic Committee for Fisheries (<https://stecf.jrc.ec.europa.eu>),
233 which provided data on fishing effort for all EU countries in hours fished per statistical
234 rectangle (111.12 km × 55.56 km). Bottom and pelagic trawl were the two dominant
235 *métiers* over the Celtic Sea (Mérillet et al., 2020).

236 We studied the distribution of sensitivity score CWM as a function of
237 environmental variables (depth, sediment, chlorophyll a and temperature), fishing
238 variables (bottom trawl, pelagic trawl) and time (year). In a preliminary step, a
239 permutation test for Moran's I statistic (Moran, 1950) indicated that spatial
240 autocorrelation was significant for sensitivity score (Moran'I= 0.29; p-value = 0.001).
241 Collinearity between variables was assessed with a variance inflation factor (VIF) and
242 a threshold of five.

243 The $\log(x+c+1)$ -transformed CWM of the sensitivity score followed a Gaussian
244 distribution and were modelled using simultaneous autoregressive (SAR) models
245 (after testing their advantage compared to GLM models with spatial terms, table S2,
246 and looking at their relationship with environmental variables Fig. S5). This family of
247 models assumes that the response at each location is a function of the explanatory
248 variables but also of neighbouring locations (Kissling and Carl, 2008). The spatial-
249 error model, which is the most reliable SAR model, captures spatial autocorrelation
250 that is not completely explained by the explanatory variables or that is an inherent
251 property of the response variable. To implement this model, we used the *errorsarlm*
252 function in the “SpatialReg” package (Bivand and Piras, 2015). A full model was built
253 with all the environmental, fishing and time variables, as well as spatial variables
254 (latitude, longitude, latitude², longitude² and latitude x longitude). The model with the
255 lowest AIC was selected using the *dredge* function (“MuMIn” R package). Temporal
256 autocorrelation in the residuals of the model was tested with a Durbin-Watson test
257 (Durbin and Watson, 1971).

258

259 2.4. Local temporal trends in the biomass of the taxa most sensitive to fishing

260 Based on a histogram, the sensitivity score distribution was examined. To
261 inform a global trend over the Celtic Sea between sensitivity and dynamics of the
262 biomass, temporal trends of the $\log(x+1)$ -transformed biomass of each taxa in the
263 whole Celtic Sea was modelled (biomasses were elevated to the whole Celtic Sea
264 following (Mahe and Poulard, 2005)), as a function of the year with a linear model
265 using a Gaussian distribution (Fig 4, Fig. S4, Table S4). Then a Spearman correlation
266 was computed between the significant slopes of the regressions of the biomass over
267 the time and the sensitivity scores (Fig. 4). Based on a histogram of the sensitivity

268 scores (Fig 4), the most sensitive taxa, which clustered apart from the other taxa (i.e.
269 before the stall in sensitivity score) were examined at a local scale to investigate
270 more precisely the link between temporal evolution of the biomass and fishing effort.
271 In that purpose, the temporal trend over 2000-2016 of the biomass of the most
272 sensitive taxa was investigated in each International Council for the Exploration of the
273 Seas (ICES) statistical rectangle.

274 Since the number of sampling sites is not homogeneously distributed across
275 rectangles, Y_i the elevated biomass of a taxa i was calculated in each rectangle r with
276 the following formula (Mahe and Poulard, 2005):

$$Y_i = \frac{1}{A} * \sum_r A_r * Y_{ri}$$

277 With Y_r the mean biomass per haul in a rectangle r , for taxa i , A_r the area of a
278 given statistical rectangle (all similar in the Celtic Sea), A the sum of the areas of all
279 the rectangles that are included or partially included within the limits of the Celtic Sea
280 considered here. The $\log(x+1)$ -transformed elevated biomass of each taxa was
281 modelled, in each statistical rectangle, as a function of the year with a linear model
282 using a Gaussian distribution. P-values associated with the coefficient of the year
283 variable were adjusted for multiple tests (Benjamini and Yekutieli, 2001). For each
284 taxon, the coefficient of the year variable was extracted when significant ($p < 0.05$).
285 We graphically examined the spatial covariation of biomass and trends in fishing
286 effort over 2000-2016 to assess whether the sampling sites that had an increased
287 biomass of the most sensitive taxa also showed a decrease in bottom trawl effort.

288 All analysis were conducted R 4.2.1 software (R Core Team, 2020).

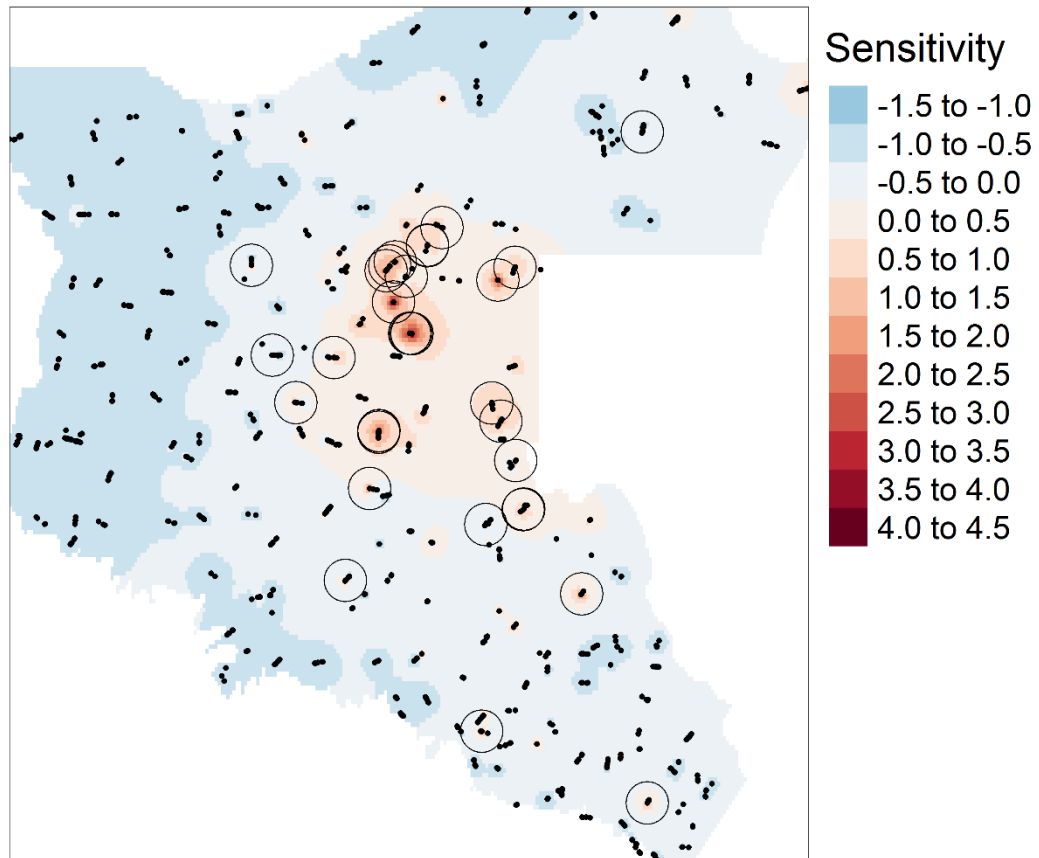
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290 3. Results

291 3.1. Assembly rules based on sensitivity score

292 Hill-Smith analysis of the selected life history traits enabled us to characterise
293 the extent to which each taxon's combination of life history traits made it sensitive to
294 fishing. The first axis (used as the sensitivity score) explained 34.3% of the total
295 variability, while the second axis explained 15.2%. The most sensitive taxa (i.e. large,
296 long-lived taxa that mature late, bear their offspring and have low fecundity) had the
297 highest sensitivity scores.

298 To distinguish the dominant assembly process between environmental
299 filtering, competition and stochasticity at each site, the CWV of the sensitivity score
300 was compared to a random CWV over the 2000-2016 period. At the majority of the
301 sampling sites (1142 over the 1175 sampling sites), the difference between the
302 observed CWV and the mean random CWV of the sensitivity score was not
303 significant, meaning that stochasticity was the dominant assembly process at these
304 sites. No sampling sites had significant negative SES values, indicating that
305 variability in sensitivity score was not significantly lower than that expected by chance
306 (i.e. underdispersed traits). Few significant positive SES values (i.e. wider range of
307 traits values than that expected by chance), i.e. 33 out of 1175, were visible at
308 sampling sites in the centre of the Celtic Sea and indicated overdispersion (Fig. 2).



309

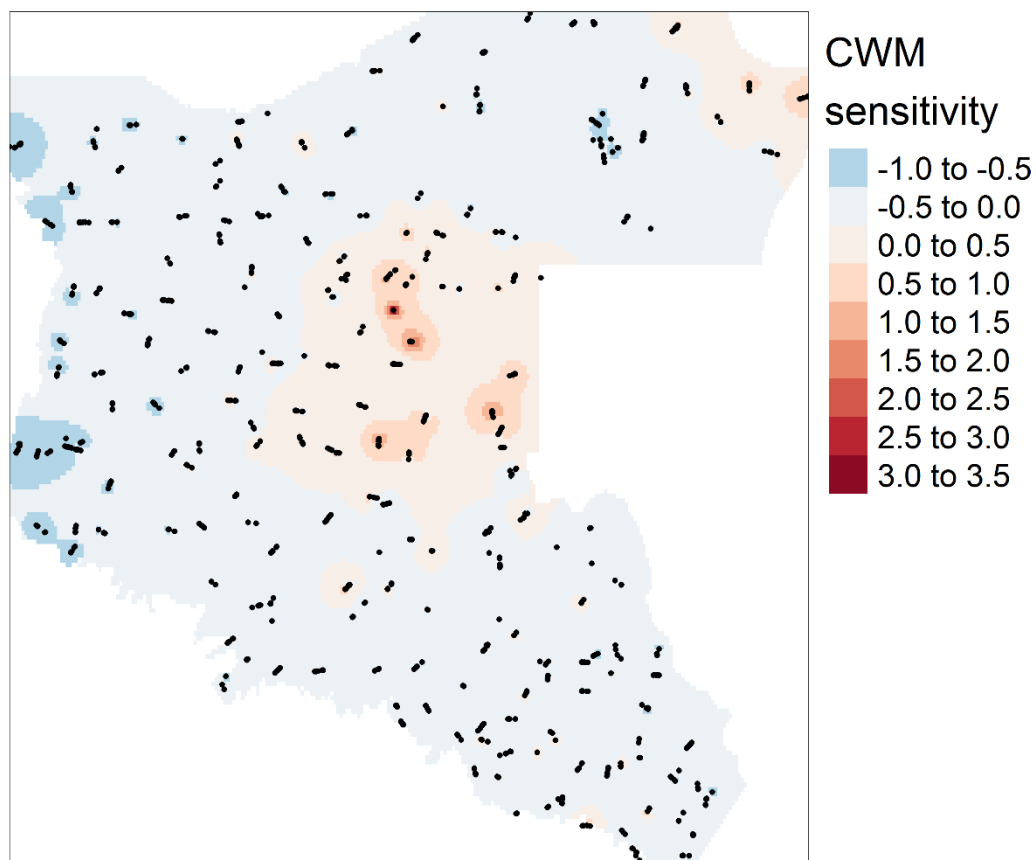
310 *Figure 2. Maps of standard effect size of the community-weighted variance (CWV) of the sensitivity to fishing*
 311 *computed from six life history traits of 101 taxa in the Celtic Sea. Sampling sites surrounded by circles show*
 312 *significant departure from the stochastic assembly process. Positive values (in red) indicate overdispersion in the*
 313 *traits and negative values (in blue) indicate underdispersion.*

314

315 3.2. Environmental drivers of the distribution of sensitivity score and traits

316 Overall, most of the Celtic Sea showed low values of sensitivity to fishing,
 317 which was indicated by the negative values of CWM of the sensitivity score (Fig. 3).
 318 The biomass of sensitive taxa to fishing was highest in the centre-east of the Celtic
 319 Sea (Fig. 3). This area also had the widest range of trait values expressed (i.e.
 320 overdispersion), indicated by the significant positive SES values of sensitivity score
 321 (Fig. 2), and the significant positive SES values associated with maximum length,
 322 age at maturity and offspring size (Fig. S2). Thus, sensitive taxa, with large maximum

323 length, age at maturity and offspring size were also present in the centre-east in
324 addition of the low sensitivity taxa present in all the Celtic Sea. Having a closer look
325 at each trait separately, we showed that only longevity showed a slightly different
326 pattern, with the narrowest range of trait values in the north and the widest in the
327 south (Fig. S2). For reproductive guild, two of the three levels (i.e. bearer and
328 guarder) had their highest proportions of biomass in the centre and extreme north-
329 east of the Celtic Sea and were nearly absent elsewhere. Thus, all three reproductive
330 guilds occurred in these two areas (Fig. S2), which agreed with the overdispersion
331 observed there (Fig. S2). Similarly, three levels of the four fecundity levels (i.e. low,
332 medium and very high) had some of their highest proportions of biomass in the
333 centre and were nearly absent elsewhere, which led to overdispersion of the
334 fecundity trait in the centre (Fig. S2).



335

336 *Figure 3. Maps of community-weighted means (CWMs) of the sensitivity to fishing computed from six life history*
 337 *traits of 101 taxa in the Celtic Sea.*

338 The VIF of the model with environmental, fishing and time variable was below
 339 5, so all variables were kept for the full model. Spatial variables were also kept to
 340 account for spatial autocorrelation. Moreover, Moran's I indicated no residual
 341 autocorrelation ($p > 0.05$) in the selected SAR model of the CWM of the sensitivity
 342 score, which was not the case for the GLM (Table S2). In addition, no temporal
 343 autocorrelation could be found in the residuals of the selected SAR model for
 344 sensitivity score (Durbin-Watson statistic = 1.40, $p\text{-value} = 1.96 \cdot 10^{-1}$), neither in the
 345 residuals of each traits modelled separately (Fig. S2).

346 *Table 2. Estimates of explanatory variables in spatial autoregressive model of the sensitivity score ($\log(x+c+1)$ -*
 347 *transformed). Only significant estimates are shown ($p < 0.01$).*

Trait	Depth	Sediment	Chlorophyll a	Bottom temp..	Bottom trawl	Pelagic trawl	Year	Lat.	Long.	Lat. ²	Long. ²	Lat. × Long.
Sensitivity score		Coarse	-7.08×10^{-3}		-4.05×10^{-6}		5.69×10^{-3}	4.20×10^{-2}	1.36×10^{-1}	-7.53×10^{-2}	-4.96×10^{-2}	7.52×10^{-3}
		Mix	-7.50×10^{-2}									
		Mud	7.54×10^{-2}									
		Sand	6.56×10^{-2}									

348

349 The spatial variables (latitude, longitude, their quadratic effects and
 350 interaction) as well as bottom trawl effort, sediment and year were significant drivers
 351 of the CWM of the sensitivity score (Table 2). Traits taken separately brought more
 352 details on which trait forming the sensitivity score responded to which variables. The
 353 models of the sensitivity score and each of the life history traits highlights the
 354 importance of the habitat, described by sediments and depth. The biomass of
 355 sensitive taxa tends to be higher on mud and sand sediments than on mix and
 356 coarse (boulders taken as a reference) (Table 2).

357 Depth was not a significant driver of the CWM of the sensitivity score, but was
358 a significant structuring variable of some of the CWMs made on the traits taken
359 separately: the relative biomass of taxa with large maximum length and high age at
360 maturity increased in shallower areas (Table S3). Conversely, the relative biomass of
361 taxa that are long-lived, bear their offspring (i.e. bearer) and have low fecundity, as
362 well as that of non-guarder taxa and high fecundity taxa, tended to increase in
363 deeper areas (Table S3).

364 All CWMs of the sensitivity score and each trait taken separately covaried
365 negatively with bottom trawl effort (Table 2 and Table S3). Areas with little bottom
366 trawl effort tended to have the highest relative biomass of large, long-lived taxa that
367 have low fecundity, mature late and give birth to large offspring. The relative biomass
368 of taxa with very high fecundity also decreased as bottom trawl effort increased.
369 Conversely, areas with large bottom trawl effort had the highest relative biomass of
370 egg-guarding taxa and high fecundity taxa. In comparison, the spatial covariation of
371 CWMs with pelagic trawl effort was significant only for the longevity trait and the non-
372 guarder level. Pelagic trawl effort had a negative influence on the relative biomass of
373 long-lived taxa but a positive influence on that of non-guarder taxa (Table S3).

374 Regarding temporal trends in CWMs in the Celtic Sea, the relative biomass of
375 sensitive taxa increased over 2000-2016 (Table 2). More precisely, the relative
376 biomass of large taxa that mature late, have low fecundity and large offspring
377 increased from 2000-2016. Conversely, the relative biomass of taxa that guard their
378 eggs and have medium or high fecundity decreased from 2000-2016 (Table S3). As
379 bottom temperature increased, the relative biomass of long-lived taxa increased,
380 while that of non-guarder taxa and taxa with very high fecundity decreased. Taxa with

381 very high and medium fecundity tended to have lower relative biomass at sites with
382 higher chlorophyll a concentrations (Table S3).

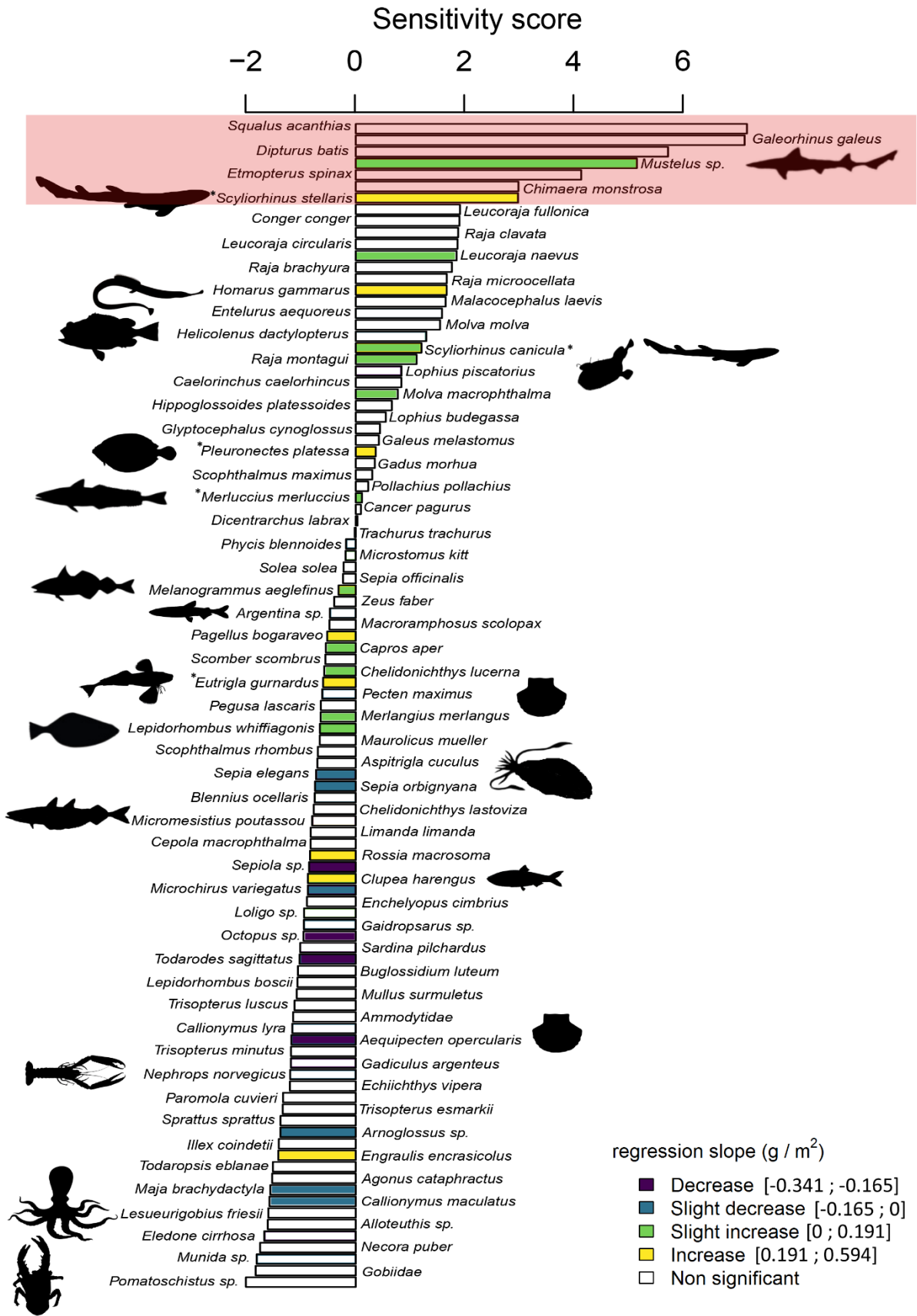
383

384 3.3. Local variation in the biomass of the most sensitive taxa in relation to local
385 fishing patterns and closure area

386 Among all taxa, the temporal trend in biomass significantly increased for 19 taxa,
387 significantly decreased for 10 taxa and had no significant trend for 72 taxa (Table
388 S4). At the scale of the Celtic Sea, biomass appeared to increase for the most
389 sensitive slow life history taxa (Fig. 4). This is confirmed by the positive correlation
390 between significant slope of the regression ($p < 0.05$) of the biomass of each taxa over
391 time and sensitivity scores (Spearman's $\rho = 0.52$; $p = 0.004$) (Fig S6).

392 Seven taxa had a distinctly higher sensitivity score than the other taxa (Fig. 4),
393 namely spurdog *Squalus acanthias*, school shark *Galeorhinus galeus*, blue skate
394 *Dipturus batis*, smooth-hound *Mustelus sp.*, velvet belly *Etmopetrus spinax*, rabbit
395 fish *Chimaera monstrosa* and nursehound *Scyliorhinus stellaris* (i.e. sharks, rays and
396 chimaeras).

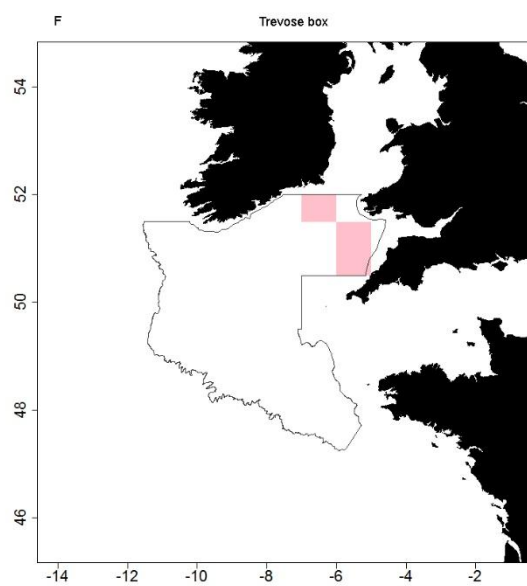
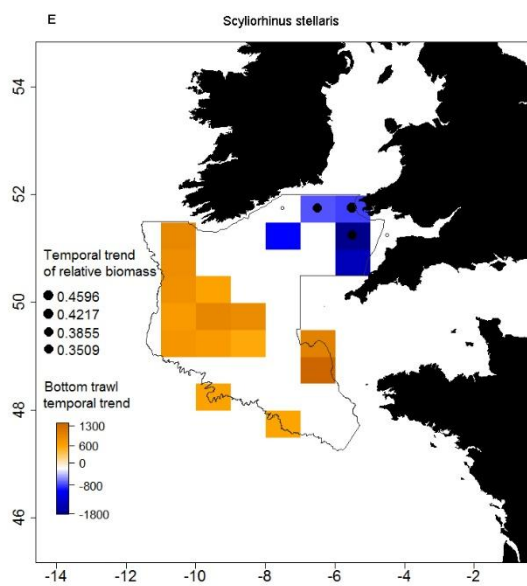
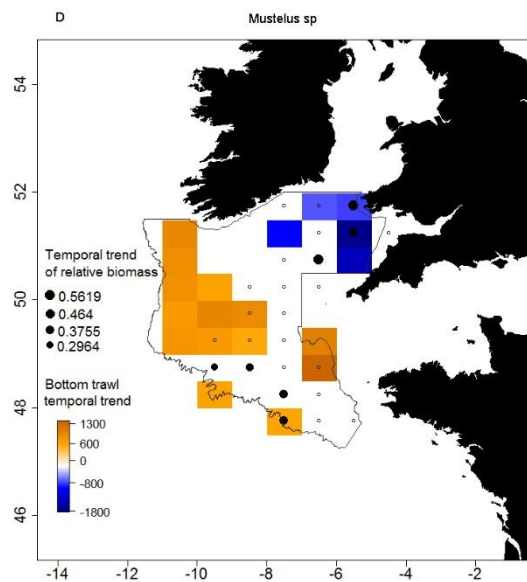
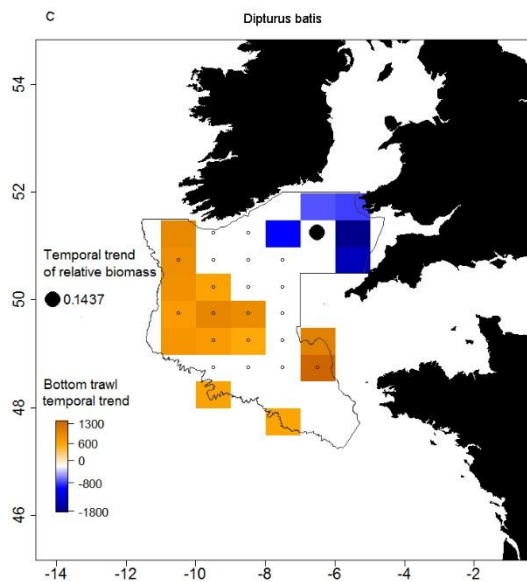
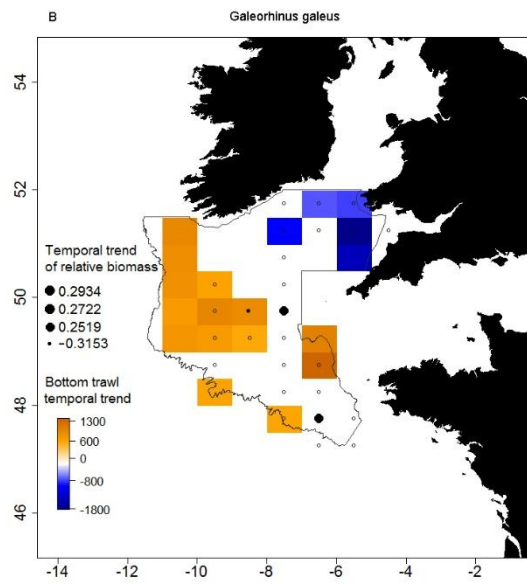
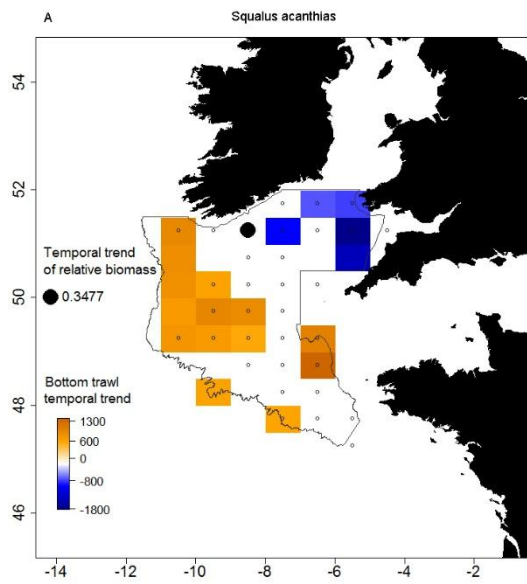
397



399 Figure 4. Sensitivity scores from Hill-Smith analysis of the six life history traits of 101 taxa in the Celtic Sea,
400 ranked from most to least sensitive to fishing. Sensitivity scores of individual taxa coloured according to the
401 quartile of the slope of the regression of biomass (g.m^{-2}) from 2000-2016. Non-significant slopes ($p > 0.05$) are
402 coloured in white. The most sensitive taxa before the stall in sensitivity values are framed in red. An asterisk
403 indicates significant slope after adjusting p-values for multiple testing.

404

405 Biomass of *Mustelus* sp., *S. stellaris* and, to a lesser extent *S. acanthias* and
406 *D. batis* significantly increased in the north-east of the Celtic Sea (Fig. 5 A. C. D. E.).
407 Areas where the increase happened correspond to the ones that experienced a
408 significant decrease in bottom trawling effort: the seasonal area closure Trevoise box
409 and its adjacent area. Nevertheless, the relationship was difficult to assess for *S.*
410 *stellaris* because of its small range in the Celtic Sea (Fig. 5 E.). Along the southern
411 border of the Celtic Sea, biomass of *Mustelus* sp. and to a lesser extent *G. galeus*
412 increased significantly in statistical rectangles with no significant trends in bottom
413 trawling (Fig. 5 B. and D.). In addition, biomass of *G. galeus* significantly decreased
414 in a statistical rectangle where bottom trawl effort significantly increased, in the centre
415 of the Celtic Sea.



417 Figure 5.(A to E) Map of the slope of the regression of biomass (g/m^2 , black circles) in each statistical rectangle
418 (111.12 km \times 55.56 km) of the Celtic Sea from 2000-2016. This figure focussed on the taxa the most sensitive to
419 fishing that have a significant variation of their biomass in at least one statistical rectangle. Small open circles
420 represent the distribution of the taxa and filled circle the significant ($p < 0.05$) slope of the regression of the
421 biomass over time. Statistical rectangles are coloured according the sign of temporal trend of bottom trawl effort
422 (hours per year within the rectangle) on time (only slopes with $p < 0.05$ are coloured). (F) Map of the seasonal
423 area closure Trevoise Box.

424

425 4. Discussion

426 To evaluate impacts of fishing on community structure, the distribution of life
427 history traits that are sensitive to fishing was studied to identify assembly rules, as
428 well as their environmental and anthropogenic drivers. At the scale of the Celtic Sea,
429 sensitivity to fishing was mostly distributed according to stochastic assembly process.

430 Significant overdispersion was mainly detected in the centre-east of the Celtic
431 Sea. Values of life history traits are more diverse than expected by chance there,
432 which suggests more diversified life history strategies. This overdispersion in traits is
433 driven by the co-occurrence of taxa with a slow life history strategy, such as the
434 common skate *Dipturus batis*, and a fast life history strategy, such as the Atlantic
435 horse mackerel *Trachurus trachurus*. Three non-exclusive deterministic processes
436 could explain the distribution of life history traits in the centre-east of the Celtic Sea:

437 (i) *Competition among coexisting taxa fosters trait overdispersion.*

438 Competition might lead to either competitive exclusion or to spatial and/or
439 temporal avoidance among co-occurring taxa (Cahill et al., 2008; Mayfield
440 and Levine, 2010). However, in the centre of the Celtic Sea were
441 overdispersion occurs, competition between fast and slow life history taxa
442 does not appear as a reasonable explanation of the large range of

443 sensitivity score expressed, as for instance skate and Atlantic horse
444 mackerels do not compete for food.

445 (ii) *Small-scale seascape heterogeneity provides a greater diversity of niches,*
446 *in agreement with the *habitat heterogeneity hypothesis* (Tews et al., 2004).*
447 We observed that sediments, which are generally homogenous throughout
448 the Celtic Sea (mud and sand), tend to be patchier where overdispersion
449 occurs (i.e. centre-east). Life history traits define one of at least five
450 dimensions of the species ecological niche (i.e. habitat, life history, trophic,
451 defence and metabolic) Winemiller, Fitzgerald, Bower, & Pianka (2015)).
452 The area where overdispersion was observed could thus provide more
453 available niches than the rest of the Celtic Sea and allow more life history
454 strategies to coexist in accordance with the limiting similarity process
455 (Macarthur and Levins, 1967).

456 (iii) *Decrease in fishing pressure alleviated the filtering imposed on sensitive*
457 *taxa.* Overdispersion might occur when new taxa with different trait values
458 arrive or due to changes in taxa biomass among trait values. For the Celtic
459 Sea, we observed stability in the taxonomic structure (no large changes in
460 biomasses of taxa) of these communities despite spatio-temporal changes
461 in anthropogenic pressures (Mérillet et al., 2020). Focusing on traits, we
462 highlight that the biomass of slow life history taxa increased over time in
463 the centre-east and extreme north-east, thereby increasing the frequency
464 of these original trait values in the community and flattening the distribution
465 of trait values. In the extreme north-east, the biomass of sensitive taxa
466 could have increased due to the decrease in fishing pressure. It is likely
467 that when fishing was still high, it acted as a major filter on biodiversity as

468 demonstrated in Guénette and Gascuel (2012). Sensitive taxa may have
469 been filtered from the areas with intensive fishing, whereas the decrease in
470 fishing allowed more diverse taxa to coexist again.

471 Stochasticity was the dominant assembly process over the majority of the
472 Celtic Sea. Assembly processes thus appeared to be dominated by demographic
473 processes (birth, death, immigration, emigration) occurring at random with respect to
474 the taxon's identity (Vellend et al., 2014). This seems in line with the high number of
475 mobile fish in the taxa studied and dominance of dispersion of egg as reproductive
476 strategy. However, this might also result from the failure to detect deterministic
477 processes (Vellend et al., 2014) which can be due to the large number of taxa in this
478 study interacting together and reacting to abiotic variables in many different ways.

479 Underdispersion (even if non-significant) observed in the most of the Celtic
480 Sea could be due to environmental filtering that selects taxa that can endure specific
481 environmental conditions. Depth, sediments, year and bottom trawl effort are the
482 variables that significantly drive the largest number of traits and have thus a
483 particularly structuring effect on their distribution. The dependence of the CWMs on
484 variables that do not vary over time at a given site (i.e. depth and sediments)
485 illustrates the strong structuring effects of habitat. For variable that vary over time and
486 space, bottom trawl effort thus appears to be a severe condition that restricts the
487 distribution of life history traits in the Celtic Sea, with a globally negative relationship
488 with the biomass of slow life history strategy taxa demonstrated in all CWMs models.

489
490 We observed temporal variation in the biomass of slow life history strategy
491 taxa that increased from 2000-2016 at the regional scale. At the scale of the Celtic
492 Sea, bottom trawling was stable over the period studied (Mérillet et al., 2020), but this

493 stability masks local differences that are visible at the scale of the statistical
494 rectangle, as showed here. Almost all significant increases in the biomass of the
495 most sensitive taxa occurred in statistical rectangles in which bottom trawling
496 decreased or showed no significant trend. This is particularly clear for *Mustelus* sp.,
497 *S. stellaris*, *D. Batis* and *S. acanthias*, whose populations increase in areas where
498 fishing pressure decreased. The biomass of taxa with a slow life history, especially
499 elasmobranchs, is higher in the centre-east of the Celtic Sea, and the highest part of
500 the increase in biomass of the five elasmobranchs occurred in adjacent areas: the
501 extreme north-east and south-west. This pattern could be due to a local increase in
502 abundance after a decrease in fishing pressure (in the north-east), but also to a
503 replenishment from the larger number of individuals present in the centre-east of the
504 Celtic Sea (Green et al., 2014). As an open sea with relatively homogenous
505 sediment, the Celtic Sea appears to be a seascape that large-bodied and mobile taxa
506 can cross easily. We hypothesize that the centre of the Celtic Sea could have
507 functioned as a refuge and then a source for recolonization of the north-east when
508 fishing pressure began to decrease. A similar recovery of a depleted population from
509 adjacent areas in a fishing ground was observed for predatory fish on the north-west
510 Atlantic shelf (Shackell et al., 2012).

511 The observed increase in sensitive slow life history taxa could be related to a
512 local decrease in fishing pressure due to management practices. In 2009, the EU
513 began to enforce its Common Fisheries Policy, which decreased overall fishing effort
514 in EU seas (Walter, 2010). In this context, fishing effort was displaced from the north-
515 east to the west and south-west of the Celtic Sea and decreased bottom trawl effort
516 in certain statistical rectangles. It may also have benefited the prey of slow life history
517 taxa, as demonstrated in Georges Bank, a formerly overexploited ecosystem east of

518 Massachusetts, USA (Mayo et al., 2014), although we did not observe an overall
519 increase in biomass of small pelagic fish. This lack of evidence may have been due
520 to incomplete sampling of pelagic communities. Moreover, the seasonal fishing
521 closures of the Trevoise Box (1st February until 31 March each year) prohibits fishing
522 activity in three statistical rectangles in the north-east Celtic Sea (30E4, 31E4 and
523 32E3). This seasonally closed area created in 2005 (European Commission, 2013;
524 ICES, 2007) has most likely prompted the recovery observed in slow life history taxa,
525 which confirms the hypothesis of the benefits of this closure (Horwood et al., 1998).
526 Indeed, we observed the largest significant decrease in bottom trawl effort and
527 increase in biomass for four of the five aforementioned elasmobranch taxa in this
528 area. This area is also a known spawning ground and nursery for many species,
529 including elasmobranchs (Potter et al., 1997), and could, in addition to serving as a
530 refuge for adults from fishing pressure, favour the replenishment of the population by
531 increasing reproductive success. The increase in biomass of slow life history taxa
532 observed in the Celtic Sea is in line with the increase in equilibrium strategy taxa (e.g.
533 elasmobranchs) observed in the North Sea (Pecuchet et al., 2017) following a
534 decrease in fishing effort and an increase in temperature.

535 A negative relationship was observed between bottom temperature and the
536 biomass of short lifespan taxa as well as very high fecundity taxa (characteristic of
537 the fast life history strategy). In addition, we also showed that taxa with a significant
538 decrease in biomass tended to be least sensitive to fishing and had fast life history
539 traits (i.e. small maximum length, short-lived, early-maturing, small offspring, non-
540 guarder and high or very high fecundity). This decrease in the biomass of fast life
541 history taxa could thus arise from the significant increase in bottom temperature that
542 occurred in the north of the Celtic Sea over 2000-2016 (Mérillet et al., 2020). This

543 decrease in fast life history taxa was also observed in the English Channel after a
544 warm phase of the Atlantic Multidecadal Oscillation (McLean et al., 2018). Fast life
545 history taxa are highly responsive to an increase in temperature due to their short
546 generation time (McLean et al., 2018). In the North Sea, mixed trends were observed
547 since the biomass of periodic strategy taxa have decreased over the past 30 years,
548 but opportunistic taxa (at the fasted end of the continuum of life history strategy) have
549 increased (Pecuchet et al., 2017). Overall, as in adjacent area, the observed life
550 history patterns in the Celtic Sea most likely result from an interplay between
551 temperature and fishing.

552

553 5. Conclusion

554 Analysis at various spatial and temporal scales enabled us to draw some
555 conclusions about the recent evolutions of sensitivity patterns to fishing in the Celtic
556 Sea. Assembly processes are mostly explained by stochasticity in the demographic
557 events. Nevertheless, environmental filtering applied by fishing pressure on the taxa
558 also appeared to have had an importance. In this historical fishing ground, fishing
559 probably acted as a filter in the north-east and centre-east of the area before the
560 beginning of the time series studied here. This filter got slowly removed allowing
561 significant limiting similarity to be revealed (in a heterogeneous habitat or from the
562 competition between taxa).

563 We showed the negative relationship between fishing effort and the biomass
564 of taxa exhibiting sensitive traits, but also the increase in biomass of the most
565 sensitive taxa from 2000-2016, in link with the creation of the Trevoise box area
566 closure. Rapid changes in the functional structure of the communities are expected in

567 the future as climate change effects become more tangible and superimpose to
568 fishing ones. Management measures leading to short-term improvement of the
569 biomass of sensitive taxa to fishing are thus urgently needed (O'Leary et al., 2017).
570 This study highlights potential positive dynamics for a group of sensitive species due
571 to a local decrease in fishing pressure. Within two decades, mitigation measures,
572 such as area closures that restrict fishing effort spatially or temporally on essential
573 habitats such as spawning and nursery grounds could significantly increase the
574 biomass of the most sensitive taxa, which can then act as a source for recolonization.
575 This positive response to recent EU policies could be a useful feedback for
576 managers. However, a continual caution during ecosystem management of fishing
577 grounds is required, as commercially fished small pelagic taxa could experience a
578 decrease in biomass in the future due to climate change and could eventually be
579 replaced by warm water pelagic taxa.

580

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586

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