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1 **Manuscript submitted for publication in Fisheries Research**

2 **Exploring the impacts of fishing and environment on the Celtic Sea**
3 **ecosystem since 1950**

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10

11 **Abstract**

12 Analyzing the long-term changes in ecosystems and disentangling the influence of overfishing and
13 the environment require historical data integration. Fisheries-independent data are available only
14 since the mid-1980s in the Celtic Sea and thus provide a short-term and truncated vision of fishing
15 impacts. We conducted a catch-based study over the 1950-2015 period. We successively (i)
16 reconstituted catch time-series, including unreported catch estimates, and studied them through a
17 trophic-spectrum approach and ecosystem indicators based on trophic level, size and species
18 diversity; (ii) estimated biomass trends of the main Celtic Sea target species from catch and effort
19 time-series, using production models that detect potential shifts in productivity; and (iii) explored
20 linkages between species productivity potential and both fishing and environment using long-term
21 time-series of large-scale climatic indices, locally observed hydroclimatic variables and plankton
22 data from the Continuous Plankton Recorder. Our results highlight that fishing has caused a drastic
23 depletion of the main exploited species in the Celtic Sea since World War II. The biomass reduction

24 of larger demersal species may reach more than 80%; additionally, this depletion occurred earlier
25 than previously thought and initiated a trophic cascade in the ecosystem. North Atlantic
26 hydroclimatic variability affected species productivity, worsening the early stock depletion while
27 potentially mitigating fishing impact in the 1990s. The common pattern in productivity changes
28 among analyzed species highlights an abrupt transition whose timing matches that of the
29 ecosystem shifts identified in several Atlantic ecosystems. Finally, we show that the recent fishing
30 pressure reduction led by the European Common Fisheries Policy initiated a partial recovery of
31 stocks and ecosystem status over the last decade.

32 Key words: Fishing impact – Celtic Sea - Catch reconstruction - Biomass production model –
33 Ecosystem regime shifts – Trophic cascade – Fish productivity

34 1. Introduction

35 The second half of the twentieth century was characterized by a dramatic increase in fishing
36 pressure worldwide (Rousseau *et al.*, 2019, Bell *et al.*, 2017), and European seas were affected too.
37 Although World War II gave a respite to European fish stocks (Letaconnoux, 1948), this respite was
38 short (Holm, 2012). Postwar fishing capacity rebuilding plans, intra-European competition and,
39 later, fleet modernization plans drove large increases in the fishing effort until the late 1980s
40 (Meuriot, 1986; Mesnil, 2008; Guénette and Gascuel, 2009). Despite the establishment of the
41 Common Fisheries Policy (CFP) in 1983 and its consecutive reforms, overfishing was not reduced
42 before the late 2000s (European Commission, 2001, 2009; Daw and Gray, 2005; Gascuel *et al.*,
43 2016). In addition to fishing, European seas have experienced major environmental changes since
44 the mid-twentieth century. Long-term variability in hydroclimatic conditions induced critical
45 changes in planktonic production (Planque and Taylor, 1998; Edwards *et al.*, 2001; Beaugrand,
46 2005), and these changes propagated through the food web to finally impact the overall dynamics
47 and productivity of Northeast Atlantic ecosystems. In particular, such changes could push some
48 ecosystems from one stable state to another through ecosystem regime shifts (Scheffer *et al.*,

49 2001; Collie *et al.*, 2004).
50 Elucidating the long-term impacts of fishing and environment on ecosystems and disentangling
51 their respective effects is a key challenge to better understanding ecosystem functioning (Kirby *et*
52 *al.*, 2009; Gaichas *et al.*, 2011; Lotze *et al.*, 2011) and providing valuable insight for fisheries
53 management (Pitcher, 2001; Borja *et al.*, 2010; Thurstan *et al.*, 2015). In this context, the analysis of
54 historical abundance trends of all ecosystem compartments is a cornerstone. By combining both
55 fisheries-dependent and -fisheries-independent information, usual stock assessments provide
56 valuable information. However, stock assessments refer to a limited part of marine resources and
57 often begin once stocks have already been intensely exploited. One way to address this issue is to
58 extend biomass estimates beyond the period covered by a stock assessment based on partial time-
59 series of catch per unit efforts (CPUEs) (Rosenberg *et al.*, 2005; Eero and MacKenzie, 2011). When
60 information is scarce, another option is to work with catch data while noting that it is influenced by
61 fishing strategies (Pauly *et al.*, 2013).

62 As one of the most exploited seas in Europe and its neighboring ecosystems that has experienced
63 major environmental changes in recent decades (Reid *et al.*, 2001; Southward, 1980), the Celtic Sea
64 likely underwent deep changes in its structure and functioning since 1950. However, these changes
65 are poorly known, and few stock assessments started before the 1980s in this area.

66 Stock assessments show that the fishing pressure has continuously increased since the mid-1980s
67 and culminated in the late 1990s when the abundance of exploited stocks reached its historical
68 minimum level (Bentorcha *et al.*, 2017; Gascuel *et al.*, 2016). Additionally, fisheries-independent
69 survey data show that fishing altered the trophic and size structures of the ecosystem (Blanchard *et*
70 *al.*, 2005; Shephard *et al.*, 2012; Pinnegar *et al.*, 2002; Gascuel *et al.*, 2016). A meta-analysis
71 performed by Rochet *et al.* (2005), as well as more recently published ecosystem models
72 (Bentorcha *et al.*, 2017; Moullec *et al.*, 2017), confirm that the Celtic Sea ecosystem has been highly
73 impacted by fishing and was still deteriorating in the mid-2000s. The latter results suggest that a
74 decrease in fishing pressure recently promoted the recovery of the ecosystem, but only to a level

75 comparable to that of the 1980s. Additionally, Guénette and Gascuel (2012) suggested that most
76 changes in the area may have occurred between 1950 and 1970; however, these analyses have
77 failed to identify the impact of environment on ecosystem functioning.

78

79 Therefore, our aim is to look deeper into the Celtic Sea history, from post-WWII fisheries
80 development to the most recent years characterized by the implementation of the F_{MSY} approach in
81 Europe and to better quantify changes induced by both fishing and environment in the ecosystem
82 after 1950. Thus, we successively (i) reconstituted catch time-series, including unreported catch
83 estimates, for all species and studied them through a trophic-spectrum approach and ecosystem
84 indicators; (ii) reconstituted effort time-series for 14 key species of the Celtic Sea ecosystem and
85 fisheries; (iii) integrated reconstructed catch and fishing effort time-series in ad hoc production
86 models to estimate biomass trends of the 14 species while exploring changes in their productivity;
87 and (iv) explored linkages between species productivity potential and both fishing and
88 environment.

89

90 2. Material and Methods

91 2.1. *Study area*

92 The Celtic Sea is a large region of the northwestern European continental shelf that spreads from
93 the western English Channel to the start of the Porcupine Bank, Southwest Ireland. The Celtic Sea
94 continental shelf displays a great variety of oceanographic conditions and habitats that result in
95 wide biological diversity (Ellis *et al.*, 2013; Martinez *et al.*, 2013). The Celtic Sea, here matching with
96 ICES Divisions 7e-j, has been a crucial area for European fishing fleets for decades and is still so.
97 With more than 420,000 tons landed yearly during the last decade, it is essentially exploited by
98 French (39% of catches for the 2010-2015 period, according to ICES statistics), Irish (21%) and UK
99 fisheries (18%). Vessels operating in the Celtic Sea use several demersal gears, including bottom

100 trawlers, beam trawlers, gillnetters, longliners and dredgers, and pelagic gears, including mainly
101 pelagic trawls (Laurec *et al.*, 1991; Pelletier and Ferraris, 2000; Marchal *et al.*, 2007). Based on the
102 targeted species, the fishing strategies result in heterogeneous exploitation of the continental shelf
103 (Sharples *et al.*, 2013; Mateo *et al.*, 2017).

104 2.2. *Catch study*

- 105 • Reported and reconstructed catches

106 Landings of all fish species between 1950 and 2015 were taken from the Statlant database
107 (available on ICES website, [ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-](https://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)
108 [assessment.aspx](https://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)), and the data for tuna-like species came from ICCAT
109 (iccat.int/en/accesingdb.html). Information on the landings of primary benthic producers was
110 issued in the literature (Arzel, 1989, 1994). The Statlant database includes only official landings;
111 thus, it underestimates the total removals. To address this issue, complementary information from
112 the Sea Around Us project (SAUP, Pauly and Zeller, 2015) was used. Catch reconstruction by the
113 SAUP for the Celtic-Biscay Shelf Large Marine Ecosystem (Miller and Zeller, 2013; Bultel *et al.*, 2015;
114 Gibson *et al.*, 2015) was used to estimate the relative quantity of unreported landings and discards
115 regarding official landings. These rates were then applied to the reconstituted landings to convert
116 them into catches. More details about Celtic Sea catch reconstitution can be found in Appendix S1.

117 For the sake of clarity in the description of the results, low catch species were pooled using the
118 trophic groups of the Celtic Sea Ecopath model developed by Moullec *et al.* (2017). The following
119 study relies on reconstituted catches, and the approach described in paragraph 2.4 will also be
120 explored using Statlant landings only.

- 121 • Catch-based indicators

122 The overall changes in catch composition were investigated by calculating Shannon's diversity
123 index (H'_y) (Shannon, 1949), the mean maximum length (MML_y) the mean trophic level (MTL_y)
124 (Jiming, 1982; Pauly *et al.*, 1998) and the high trophic level Indicator (HTI_y) (Bourdaud *et al.*, 2016)

125 for each year y . H' represents the species diversity and can identify whether fisheries rely on few
 126 species or exploit a wide range of species. The MML quantifies the relative importance of small and
 127 large species and is expected to decrease due to fishing, which drives down the proportion of
 128 species with large asymptotic size and slow growth and maturation. The last two indicators are
 129 related to the food-web structure. The MTL and the HTI, which correspond to the fraction of top
 130 predators in the total catch, also decline with increasing fishing impact.

131 The indices are calculated as follows:

$$132 \quad H'_y = \sum_S (P_{s,y} * \log_2(P_{s,y})) \quad (\text{eq.1})$$

133 where $P_{s,y}$ is the proportion of the species s in the total landings of year y .

$$134 \quad MML_y = \frac{\sum_S (L_{\infty_s} * Y_{s,y})}{\sum_S (Y_{s,y})} \quad (\text{eq.2})$$

135 with L_{∞_s} the asymptotic length of species s , as reported in FishBase (Froese and Pauly, 2016), and
 136 $Y_{s,y}$ the catches of species s in year y . This index excludes invertebrate species.

$$137 \quad MTL_y = \sum_S \frac{Y_{s,y} * TL_s}{Y_y^{tot}} \quad (\text{eq.3})$$

138 where TL_s were estimated from the Celtic Sea Ecopath model for monospecific groups and from
 139 FishBase for other species; Y_y^{tot} is the total catch amount in the Celtic Sea.

$$140 \quad HTI_y = \frac{Y_y^{TL \geq 4}}{Y_y^{TL \geq 2}} * 100 \quad (\text{eq.4})$$

141 where $Y_y^{TL \geq 2}$ and $Y_y^{TL \geq 4}$ are the total catches in year y of species with a TL higher than or equal to 2
 142 and 4, respectively, in the Celtic Sea.

143 Finally, to obtain a more synthetic overview of changes in the trophic composition of catches, the
 144 trophic spectra of mean yearly catches (Gascuel, 2005; Gascuel *et al.*, 2005) were built by decades
 145 using the ET-Transpose function of the EcoTroph R package, which distributes each group/species
 146 on a range of TLs according to its own trophic variability (Gascuel *et al.*, 2011; Colleter *et al.*, 2013).

147 2.3. Trends in fishing pressure for the main targeted species

148 A standardized index of species-specific fishing pressure was estimated over the period of 1950-
 149 2015 for 14 species among the most exploited species in the Celtic Sea and those currently
 150 assessed by ICES. These species were selected because enough information can be found in the
 151 literature to reconstruct past fishing pressures; the species include cod (*Gadus morhua*), hake
 152 (*Merluccius merluccius*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*),
 153 sea bass (*Dicentrarchus labrax*), anglerfish (*Lophius piscatorius* and *L. budegassa*), megrim
 154 (*Lepidorhombus whiffiagonis*), sole (*Solea solea*), plaice (*Pleuronectes platessa*), mackerel (*Scomber*
 155 *scombrus*), horse mackerel (*Trachurus trachurus*), pilchard (*Sardina pilchardus*), herring (*Clupea*
 156 *harengus*) and Norway lobster (*Nephrops norvegicus*). These species account for 57% of the
 157 landings during the study period and are assumed to provide an informative snapshot of changes in
 158 the Celtic Sea fishery.

159 For the recent period, the F estimates available from ICES stock assessments, denoted F_y^{ICES} , are
 160 the most reliable index of fishing pressure. To fill the gap between 1950 and the starting year of
 161 assessments, a search for data on species-specific fishing effort was first conducted. The ancillary
 162 documents and statistics that were gathered enabled the production of the nominal fishing effort
 163 time-series, E_y^{nom} (see Appendix S1 for methodological description), and these time-series were
 164 converted into effective fishing effort time-series using the mean annual rate of increase in fishing
 165 efficiency, α (Gascuel *et al.*, 1993). α allows us to consider changes in fishing efficiency related to
 166 innovation in fishing technologies (Fitzpatrick, 1996; Marchal *et al.*, 2007), and its value is defined
 167 according to the empirical equation proposed by Pauly and Palomares (2010). Effective efforts
 168 were expressed as a fishing mortality, F_y , by standardizing E_y^{nom} and F_y^{ICES} over the first three
 169 years of the stock assessment, as follows:

$$170 \quad F_y = \begin{cases} \frac{\text{mean}_{i=n:n+2}(F_i^{ICES})}{\text{mean}_{i=n:n+2}(E_i^{nom})} * E_y^{nom} * (1-\alpha)^{n-y}, & y < n \\ F_y^{ICES}, & y \geq n \end{cases} \quad (\text{eq.5})$$

171 where n is the first year of the assessment. Sensitivity analyses of the final results to the poorly
172 known parameter α were conducted using $\alpha \pm 50\%$. More details on fishing effort reconstruction
173 are provided in Appendix S1.

174 2.4. Biomass trends for the main targeted species

175 For the 14 selected species, the time-series of catch and fishing pressure were used to fit the
176 surplus biomass production model over the whole 1950-2015 period. Additionally, to estimate
177 biomass trends since 1950, the approach we developed enables the detection of long-term
178 changes in the productivity potential of each species.

- 179 • Formulation of the surplus production model

180 Surplus production models assume that stock productivity depends on its abundance. Regardless of
181 the initial conditions, the biomass of a stock fished with a constant effort tends to an equilibrium
182 state determined by the fishing pressure level. According to the Fox model (Fox, 1970), biomass at
183 equilibrium, B^{eq} , can be expressed as a function of the fishing mortality, F , as:

$$184 \quad B^{eq} = \frac{e \cdot MSY}{F_{MSY}} \cdot e^{-\frac{F}{F_{MSY}}} \quad (\text{eq.6})$$

185 where MSY is the maximum sustainable yield, which can be considered as a proxy of the
186 productivity potential of the stock, and F_{MSY} is the fishing mortality consistent with achieving the
187 MSY .

188 Though this equilibrium situation never occurs in reality (Hilborn and Walters, 1992), Fox (1975)
189 proposed to fit the model to observed abundance and effort data using a “pseudo-equilibrium”
190 method. This empirical approach, considered as more robust than dynamic production models
191 (Fonteneau *et al.*, 1998; Meissa *et al.*, 2013), assumes that the abundance at year y (B_y) is in
192 equilibrium with the cumulative fishing mortality (F_{Fox}) over the k previous years in such a way that:

$$193 \quad B_y = \frac{e \cdot MSY}{F_{MSY}} \cdot e^{-\frac{F_{Fox} y}{F_{MSY}}} \quad (\text{eq.7})$$

194 where MSY is the parameter to estimate, F_{MSY} is taken from the ICES stock assessments (current
 195 estimates or proxy, or older estimates when not available), and F_{FOX_y} is a linear combination of
 196 fishing mortality (F_y) over the k previous years:

$$197 \quad F_{FOX_y} = \frac{F_{y-k} * 1 + \dots + F_{y-1} * (k-1) + F_y * k}{1 + \dots + (k-1) + k} \quad (\text{eq.8})$$

198 k is related to the number of main exploited age classes and is conventionally fixed to 2 for small
 199 pelagic species and 3 for other species.

- 200 • Integration of changes in species productivity potential

201 Usually, surplus production models assume that fishing pressure drives changes in species
 202 abundance, in turn modifying the products according to a specific relationship. Hereafter, we
 203 considered that the environment could affect production by inducing a shift from one biomass-
 204 productivity relationship to another. This effect was integrated in our approach following Fréon
 205 (1988), who assumed that the environment impacts both the carrying capacity and the rate of
 206 population increase (K and r , respectively, while maintaining $\ln(K)/r$ constant), resulting in a time-
 207 varying MSY within the Fox model (while one F_{MSY} value per productivity regime would also be
 208 required within Schaeffer's model; Fréon, 1988). Temporal changes in the MSY value were
 209 postulated to follow regime-like dynamics. The timing of shifts in the productivity potential was
 210 investigated and integrated into the surplus production model to estimate one different MSY for
 211 each putative regime.

212 MSY shifts identification was based on rearranged eq.9:

$$213 \quad \ln(MSY) = \ln(B_y) + \ln(F_{MSY}) + \frac{F_{FOX_y}}{F_{MSY}} + 1 \quad (\text{eq.9})$$

214 Eq.9 implies that a shift in the MSY is consistent with a shift in the right-hand side of the equation.
 215 To identify productivity regimes prior to any fit and because B_y was available only once the model
 216 was fitted, the timing of potential MSY shifts was explored using observed data and investigating

217 shifts in the $\left(\ln(B_y^{obs}) + \ln(F_{MSY}) + \frac{F_{FOXy}}{F_{MSY}}\right)$ time-series, where B_y^{obs} is calculated as the ratio
218 between the reconstructed Y_y and F_y .

219 Breakpoints in these time-series were detected using the STARS method (Rodionov, 2004)
220 parameterized for a cut-off length of 10 years and a probability level set to 0.05. A “pre-whitening”
221 procedure was applied prior to running STARS to avoid potential misinterpretation of stochastic
222 fluctuations as regime shifts (Hsieh *et al.*, 2005; Rodionov, 2006). STARS was executed under the R
223 software using the function developed by Seddon *et al.* (2014).

224 • Fit of the model

225 In view of a parsimonious approach, shifts identified through data analysis were integrated in our
226 approach only if they statistically improved the surplus biomass production model. Thus, by
227 including or excluding breakpoints among those identified, we listed all potential partitions of the
228 MSY regime (hence ranging between 2 and the number of regimes identified through data analysis)
229 and fitted one model for each of them.

230 For all considered species and possible partitioning of MSY regimes, the surplus biomass
231 production model defined in Eq. 7 was fitted to the observed 1950-2015 time-series of biomass
232 B_y^{obs} (calculated as the ratio between the reconstructed Y_y and F_y) and Fox’s fishing mortality (F_{FOXy})
233 using the maximum likelihood method and assuming a lognormal distribution of the residuals. The
234 fit was performed using weighted nonlinear least squares regression. Note that in our study, the
235 Y_y/F_y ratio was preferred to the ICES estimates of biomass because the Celtic Sea area did not
236 systematically match the spatial extent of the assessed stocks.

237 Finally, the Akaike criterion (Akaike, 1974) was used to select the regime shift combination leading
238 to the best surplus production model. Once the model was fitted, the B_y values were predicted
239 over 1950-2015 from Eq. 9 using the MSY estimates, F_{FOXy} , and F_{MSY} .

240 A sensitivity analysis to the hypothesis of regime shift existence in productivity potential was
241 conducted by comparing the results to those that could be obtained under the hypothesis of (1) a
242 constant productivity potential defined by a single MSY and (2) a productivity potential with
243 continuous and monotonous change. The latter was modeled by expressing the MSY at year y as
244 the product of an initial value MSY_0 and of an annual multiplier $m_y = (1 - \beta)^{y-1950}$, where β is a
245 yearly change rate to be estimated.

246 *2.5. Linking changes in species productivity potential to environmental* 247 *variables*

248 To explore common patterns in the variability of productivity potential among the 14 selected
249 species and to identify the drivers of changes, we performed principal component analysis (PCA).
250 Years were considered as statistical individuals, species productivity potential values were
251 variables, and environmental data were supplementary variables. Environmental data included
252 local biotic data from the Continuous Plankton Recorder survey and abiotic variables reflecting
253 hydroclimate conditions at the local or regional scale. We also used egg and larvae counts from the
254 CPR survey as potential indicators of overall fish productivity in the Celtic Sea (all variables are
255 summed in Tab. 1). Based on preliminary tests, correlations with the principal component of PCA
256 on productivity potentials were analyzed with a 3-year lag. This choice is consistent with the fact
257 that the environment mainly affects early life stages (through recruitment, growth or modification
258 of the spawning feature of parents), thus delaying the observation of any effect in catches and
259 estimated productivity potential. The environmental variables, their running means and their pair-
260 correlations are plotted in Appendix B Fig. B1 and B2.

261 3. Results

262 3.1. *Catch reconstruction*

263 The relative importance of unreported catches declined over the study period, from 50% of the
264 reported landings in 1950 to 10% in 2015 (Fig. 1-A). This trend was due to the reduction in the
265 proportion of unreported landings, while the global discard rate remained quite stable (near 10%,
266 in spite of a late increase in demersal fish). Despite such variations, trends in the Statlant landings
267 and SAUP catches were similar. Due to their large and highly variable landings, pelagic species
268 shape the temporal profile of catches (Fig. 1-A, B). Mackerel, horse mackerel, and boarfish have
269 followed each other as dominant species in catches since the 1970s. Mackerel and horse mackerel
270 catches peaked in 1976 and 1995, respectively, while boarfish appeared in statistics in 2003 and
271 was the most fished species in the Celtic Sea in the late 2000s. Catches of demersal species (Fig. 1-
272 C) progressively increased after 1950, peaked the first time in 1972-1976, culminated in the 1990s,
273 and then declined by 30% between 1997 and 2008. Since then, demersal species have returned
274 their 1980s level. The proportion of emblematic species such as hake, cod, whiting and sole (i.e.,
275 the primary exploited demersal species after WWII) progressively declined while fisheries started
276 targeting new species such as anglerfish and pout in the 1970s or smaller demersal species in the
277 1980s. Invertebrates made important contributions to catch diversification (Fig. 1-D). Their removal
278 continuously increased until 2006, and they were driven by spectacular bivalve fisheries
279 development after 1971 and by a gradual increase in cephalopod and crustacean exploitation.

280 3.2. *Trophic and sized-based analysis of catches*

- 281 • Ecosystem indicators

282 Both trophic and size-based indicators (Fig. 2) displayed similar declines between 1950 and 2010.
283 The mean trophic level (MTL) was reduced by 0.38 and the mean maximum length (MML) was
284 reduced by 25 cm, while the proportion of predators in the catch (HTI) declined by more than half.

285 Thus, fisheries targeted species with a smaller size and lower trophic level over time. This trend is
286 explained by both the greater amount of pelagic fish and invertebrate removals and the changes in
287 the composition of demersal fish catches; additionally, when these values were calculated
288 excluding horse mackerel and mackerel species, the MML increased up to 88 cm in 1975 but then
289 declined by more than 40 cm over the next 25 years. The Shannon diversity index confirms the
290 catch diversification. Setting aside its temporary drops due to peaks in horse mackerel and
291 mackerel catches, the value showed a continual increase over the study period, highlighting a
292 dramatic transition from low to high diversity in targeted species.

293 All trophic and size-based indicators increased after 2010, thus exhibiting values close to those
294 observed in the late 1980s. Such changes were driven by the increasing catches of large and/or
295 high-TL demersal species (e.g., haddock, anglerfish, and hake).

296 • Trophic spectra

297 The trophic spectra point to the main changes in catch patterns (Fig. 3). Spectra were split into two
298 main areas: around a TL of 2 for primary consumers (e.g., shellfish such as great scallop or blue
299 mussel) and from a TL of 3.0 to a TL of 4.7 (Fig. 3-A) for other species. Since 1950, catches have
300 always been dominated by TLs of approximately 3.6 (i.e., mainly small pelagic species), but several
301 changes occurred over the study period. Catches in primary producer (TL=2) were almost negligible
302 until the late 1970s, and then they strongly increased. At low TLs (2.8-3.2, i.e., small crustaceans
303 and gastropods), catches continuously increased until the 2000s, when they were 3.5 times larger
304 than the value in 1950. Catches of intermediate TLs of approximately 3.6 reached large values in
305 the 1970s (mackerel) and 1990s (horse mackerel), and the values more than doubled at the end of
306 the period compared to the value of the 1950s. Higher TLs between 4.0 and 4.5 (i.e., demersal fish)
307 showed a two-phase trend marked by an initial increase until the 1990s, followed by a return to a
308 situation equivalent to the 1970s. In summary, the exploitation of the Celtic Sea developed on all

309 components of the ecosystem between 1950 and 2015 and was particularly enhanced for low TL
310 resources.

311 3.3. *Fishing pressure*

312 The mean time-series of reconstructed fishing mortality for the 14 selected stocks (Fig. 4)
313 highlighted a dramatic increase in the fishing effort since 1950 marked by the overrun of the mean
314 F_{MSY} in 1978 and a peak in 1991. Over this period, the mean fishing mortality increased
315 approximately 12-fold (between 8 and 18 for the extreme values assumed for the fishing efficiency
316 increasing rate, α) to reach a value 1.7 times the mean F_{MSY} . Despite the major European
317 decommissioning plans that followed (e.g., the French Mellick plan in 1991), fishing mortality was
318 quite stable until 2005; then, the value declined by more than 30% in just 5 years before stabilizing
319 at approximately 1.1 times the mean F_{MSY} over the last 4 years. The smoothed trend of the mean
320 fishing mortality hides a large variety of fishing mortality trajectories (e.g., early exploitation for
321 cod, later for anglerfish and sea bass) and mean values (the lowest for pilchard and the highest for
322 hake).

323 3.4. *Biomass reconstruction*

- 324 • Fox model fit and regime shifts detection

325 The Fox model fitted correctly to all species, highlighting that abundances were mainly regulated by
326 fishing (models fits in Appendix C). The best fits of the final model were obtained for hake, cod,
327 whiting, sole, plaice and Nephrops (R^2 values higher than 0.8, Tab. 1), while a poor fit was observed
328 only for haddock ($R^2 = 0.37$). All the studied species displayed shifts in their productivity potentials
329 (Fig. 5) that explained abundance variability better than the constant productivity scenario (AICs in
330 Tab. 1). These shifts suggest that fishing was not the only driver of changes in abundance. Some
331 species presented one shift, pulling apart two long periods of different productivity potential (e.g.,
332 herring and haddock). Others exhibited several shifts in productivity potential during the study
333 period. For some species (e.g., megrim and sea bass), successive regimes followed one other in a

334 monotonous trend. Regime shifts can also be “punctual” (e.g., mackerel and Nephrops), suggesting
335 a temporary perturbation (favorable or not) prior to an apparent return to standard conditions. To
336 finish, some regime shift successions form smooth fluctuations (e.g., hake, cod, and whiting).
337 According to these cases, changes in species productivity potential were either synchronic or not,
338 with periods of high fishing pressure, potentially favoring or preventing a decline in stock
339 biomasses.

340 • 1950-2015 biomass trends for the studied species

341 The fitted production models highlight a global decline in fish biomass since 1950 (Fig. 5). This
342 reduction in the abundance of Celtic Sea stocks is a direct consequence of the post-World War II
343 rise of fishing pressure in the area. The rate of decline and its timing differ according to the
344 exploitation history of each stock. Demersal species that were already commonly targeted in the
345 1950s (i.e., cod, hake, whiting, sole, and plaice) showed the steepest decrease in biomass. Over 30
346 years, these values have fallen to between 15% and 25% of their 1950 levels, while some species,
347 such as sole or hake, continued to decline and bottomed out during the 1990s. Demersal species
348 that have been targeted more recently (i.e., anglerfish, megrim or haddock and, one decade later,
349 sea bass) also displayed a similar decline in biomass, but this decline was delayed and of lower
350 amplitude. For 75% of the studied species, the lowest biomass levels were reached between the
351 early 1990s and the mid-2000s.

352 Since the late 2000s, all demersal fish species have shown increasing biomasses, suggesting a stock
353 recovery. The intensity of this recovery is highly variable according to species and is influenced by
354 their productivity potential regimes. Anglerfish, megrim, hake, and haddock appear to benefit from
355 both declining fishing pressure and favorable environmental conditions and consequently display
356 the most impressive recovery among the studied species. Biomass trajectories of pelagic species
357 exhibit more complex trends because of their higher sensitivity to environmental conditions and to
358 their highly variable fishing intensity throughout the studied period. Nonetheless, they all present

359 decreases in biomass over the whole period and no particular improvement in abundance, except
360 for herring.

361 The mean trend of the biomass for the 14 studied species, expressed in relative values (Fig. 5),
362 shows an especially fast and strong decrease over the 1950s and 1960s. Compared to 1950, the
363 mean stock biomass was reduced more than four-fold in the 1990s but has increased by
364 approximately 40% over the last ten years.

365 *3.5. Productivity regime shifts and link to environmental variations*

366 The overall productivity potential of the 14 studied species fluctuated over time, peaking in the
367 1970s and the 1990s, and there was no clear trend over the entire period (Fig. 6A). In contrast, the
368 mean value of the MSY/MSY_{1950} ratio increased by 50% over the study period. This trend was due
369 to the increase in productivity potential observed for numerous low productivity and low
370 abundance species, while a decrease occurred for a few abundant and more productive species,
371 therefore leading to the overall stability observed since 1950 at the ecosystem level.

372 The first two principal components of the PCA performed on the productivity potential explained
373 64% of all variability of the data and highlighted the similarities and divergences among species.
374 PC1 compares species with increasing productivity potential over the study period (i.e., gadoids,
375 anglerfish, sea bass, and megrim) to species with decreasing productivity potential (i.e., herring,
376 pilchard, and sole) (Fig. 7). Plotting the PC1 scores against time (Fig. 6-B) highlights a transition
377 period that initiated in the late 1970s and ended in the late 1980s, when major shifts occurred
378 toward higher (hake, cod, whiting, haddock, megrim, and plaice) or lower (pilchard and mackerel)
379 productivities (Tab. 1). PC2 splits each period before and after the 1980s, in two subperiods. Two
380 additional transition phases characterized by declining productivities are thus identified: one in
381 approximately 1960 (for hake, whiting, sole, plaice, pilchard, and lobster) and a second in
382 approximately 2000 (for hake, cod, whiting, horse mackerel, and plaice). The two-dimensional
383 space defined by the first two PCA dimensions (Fig. 7) draws groups of similar years regarding

384 productivity potential. These groups broadly correspond to decades, and the diametrical
385 opposition of the 1950s and the 2010s highlights that these two decades were particularly
386 dissimilar in terms of productivity potential.

387 Numerous biotic and abiotic parameters computed as supplementary variables were highly
388 correlated with PC1 (corr > 0.4, Fig. 7) and presented a marked increase or decrease over the study
389 period. Thus, the first PC, linked to the transition period of the 1980s, was positively correlated
390 with parameters related to the wind regime (corr=0.93 and 0.65 with the wind speed and the
391 northward westward wind component, respectively) and the Gulf stream index (0.59) and
392 negatively correlated with the sea surface salinity (SSS, -0.62) and several biotic variables (0.47, -
393 0.58 and -0.59 with phytoplankton color index, small copepods abundance, and larvae abundance,
394 respectively). This result suggests a major change, arising around the 1980s, in the environment of
395 the Celtic Sea ecosystem, toward more turbulent conditions, less saline conditions, and, in spite of
396 the lower correlation with SST, warmer water associated with great changes in small zooplankton
397 abundance (Appendix B Fig. B.1). On PC2, which was mainly related to the late 1960s, 1980s and
398 early 2000s changes in fish stock productivity, the NAO was by far the most correlated
399 environmental variable (corr=0.80), and it likely had a relationship with its strong and long-term
400 contrasts over the study period (Fig. 6-C, and Appendix B Fig. B.1). Despite the shorter time-series
401 available (n=55 once lagged), PC2 also seemed to be linked to mesozooplankton abundance and
402 composition because it was negatively correlated with the total large copepod and *Calanus*
403 *helgolandicus* species abundances (-0.65 and -0.58, respectively) and positively correlated with
404 *Calanus finmarchicus* abundance (0.34).

405 4. Discussion

406 4.1. *Capacities and limits of the data reconstruction and biomass*

407 *production model*

- 408 • Biomass production model.

409 In a first attempt to estimate the biomass trends for the main exploited species since 1950, the
410 catch-based dynamic production models developed by Martell and Froese (2013) and Froese *et al.*
411 (2017) were considered. These methods provided reliable estimates of reference points but did not
412 appear to handle stock dynamics unrelated to fishing well. They resulted in biomass trends that
413 were particularly smooth and failed to reproduce observed abundance patterns when catch time-
414 series displayed few exceptionally low or high values (see applications to the Celtic Sea stocks in
415 Froese *et al.*, 2017). By incorporating potential changes in productivity potential, the method we
416 developed overcame this issue but also allowed integration of local knowledge on fishing effort.

- 417 • Catch data reconstruction.

418 Statlant file provided by the ICES provided catches for the overall ecosystem compartments. The
419 main drawbacks of this database lie in the spatial allocation of catches, the lack of information for
420 some underreported species, and the lack of discard estimates. Catch data are treated by carefully
421 working at the spatial reallocation and searching complementary information on particular species
422 and crosschecking catch time-series with national databases; this method allows us to assume that
423 our catch reconstruction is the best that can be currently done with existing data. Additionally, the
424 integration of SAUP data into such modeling approaches is quite rare and provides an added value
425 to our study (Zeller *et al.*, 2016).

426 Sensitivity analysis showed that the estimated biomass trajectories were very similar after 1970 for
427 models using either SAUP or Statlant data. However, SAUP-based models consistently produced
428 steeper biomass declines with the decrease in unreported catches, hence providing a
429 supplementary argument for the usefulness of the integration of unreported catches in such

430 approaches. In a complementary analysis, however, catch data could also be compared to other
431 worldwide catch databases (Watson *et al.*, 2017).

432 • Fishing pressure.

433 The model appeared sensitive to the assumed value for α , defining the yearly rate of increase in
434 fishing efficiency. Assuming lower or higher values for α ($\pm 50\%$) led to lower and higher mean
435 biomass estimates in 1950 (-30% and + 60%, respectively). Nonetheless, the overall decrease in the
436 abundance of exploited stocks between the 1950 and the late 1990s remained in the same order of
437 magnitude regardless of the value of α considered (from a 3-fold to a 7-fold reduction). In addition,
438 the values of α calculated according to Pauly and Palomares (2010) seemed to be plausible and
439 even conservative (Villasante and Sumaila, 2010). Furthermore, Millischer *et al.* (1999) estimated
440 an α value of 12% for the French fleet from Concarneau targeting cod in the Celtic Sea over 1983-
441 1994.

442 The process of rebuilding fishing effort time-series in a data-poor context produces large
443 uncertainties. In our case, this uncertainty was higher for pelagic species, whose activity is highly
444 dependent on seasonal and environmental conditions. In the case where several independent
445 time-series of fishing effort are available from the literature for a given species, uncertainty might
446 be assessed through bootstrapping procedures. However, the various time-series usually have
447 different levels of reliability; thus, we preferred to select the most reliable one for each species and
448 time period based on expert judgment. Analyzing the sensitivity of the final results to a large range
449 of α coefficient values is assumed to be sufficient to explore the uncertainty of the trends in fishing
450 efforts.

451 • Productivity changes.

452 The “reference”, “continuous” and “constant” scenarios on changes in productivity potential
453 provided similar estimates of biomass for 1950 (Appendix, Fig. D1). The main difference, however,
454 was in the 1950-2015 biomass trajectories, with the reference scenario producing more realistic
455 trends and statistically better fits (see Tab. 1). Regime-like responses in fish productivity could

456 notably reflect shifts in recruitment (Ottersen *et al.*, 2013; Kell *et al.*, 2016), growth (Clausen *et al.*,
457 2018) and survival (Mueter *et al.*, 2007). Many studies confront two hypotheses about fish stock
458 productivity: productivity is determined by the spawning stock size (i.e., standard surplus
459 production model) vs productivity is determined by the environment, notably following regime-like
460 dynamics (Gilbert, 1997; Szuwalski *et al.*, 2014). Here, we proposed a more conservative option
461 corresponding to the mixed hypothesis tested by Vert-pre *et al.* (2013) in their meta-analysis,
462 which proved to be relevant for a substantial proportion of analyzed stocks. The amplitudes of the
463 shifts identified in our study were high, but they were globally in the same range of values as those
464 of MSY values determined by Clausen *et al.* (2018) for North Sea species (up to 68% variation in 30
465 years).

466 4.2. *The early alteration of the ecosystem: a fishing-induced trophic* 467 *cascade?*

468 As in many ecosystems worldwide, the dramatic expansion of fishing during the second half of the
469 twentieth century has deeply impacted the structure and functioning of the ecosystem (Myers and
470 Worm, 2003; Tremblay-Boyer *et al.*, 2011; Christensen *et al.*, 2014). Fishing pressure has constantly
471 increased in the Celtic Sea since 1950 and culminated in the early 2000s, subsequently driving
472 down the biomass of exploited species, with declines up to eight-fold for some of them. A
473 substantial part of the biomass decline occurred between 1950 and 1980, highlighting an early
474 alteration of the ecosystem and providing new evidence of shifting baselines in European seas
475 (Pauly, 1995; Guénette and Gascuel, 2012).

476 Such an impact of fishing may have cascaded through the food web. Among the main exploited
477 species in 1950, hake, cod, whiting and megrim are important predators in the Celtic Sea, and they
478 structure the food web through top-down control. The drastic reduction in their abundance must
479 have benefitted their prey, in particular, small pelagic species, which are known to be sensitive to
480 fishing-induced predation release (Daskalov, 2002; Frank, 2005; Savenkoff *et al.*, 2007). This result

481 could explain the upward shifts in mackerel productivity potential and biomass in the late 1960s,
482 which indicated a shift toward a more pelagic-dominated ecosystem. The outburst in pelagic fish
483 was concomitant with a decrease in the abundance of copepods (especially those smaller than 2
484 mm, SmCop in Appendix B Fig. B.1), the primary food source of adults and larvae, and an increase
485 in phytoplankton abundance (two-fold increase in the phytoplankton color index PCI, Appendix B
486 Fig. B.1). These opposite abundance trends between successive trophic levels suggest a fishing-
487 induced trophic cascade (Frank, 2005).

488 This potential trophic cascade may have impacted fishing. Because the outburst was
489 contemporaneous with main demersal stock depletion, pelagic fish may have been considered as
490 an alternative fishing target, resulting in a transfer of fishing effort (Lockwood and Johnson, 1976).
491 The depletion of historically targeted species also affected the diversification in fish production,
492 shifting toward few large fish species of lower commercial value at that time (i.e., anglerfish) and
493 mainly toward low TL and small demersal fish and crustaceans (Pinnegar *et al.* 2002, Gascuel *et al.*
494 2016). These patterns would suggest a significant alteration of the Celtic Sea trophic structure
495 typical of the “fishing down the marine food-web” (Pauly *et al.* 1998); however, they patterns may
496 have resulted from independent changes in fishing strategies, hence indicating the co-occurrence
497 of “fishing through the marine food-web” (Essington *et al.*, 2006).

498 Although pelagic fish have dominated the biomass in the Celtic Sea since the early 1970s, several
499 species have succeeded in a “pelagic waltz”. Quickly overexploited, mackerel biomass severely
500 declined in the early 1980s (Lockwood and Shepherd, 1984; Hawkins *et al.*, 2003). Horse mackerel,
501 which was mainly a bycatch at the mackerel fishery apogee, likely benefitted from the vacant niche
502 left by mackerel and turned into a new target species of pelagic fleets (Eaton, 1983). Once horse
503 mackerel were depleted, especially after 2000, boarfish became the most fished pelagic species.

504 4.3. *The influence of multi-decadal variability of Atlantic hydroclimate*

505 Confirming insights from a previous trophic modeling work, the productivity of the Celtic Sea
506 ecosystem appears to be under the influence of North Atlantic conditions. Positive and negative
507 phases of the NAO match favorable and unfavorable periods for most gadiformes (i.e., cod, hake,
508 and whiting), flatfish species (i.e., sole and plaice), and horse mackerel. The NAO has been shown
509 to affect fish population dynamics for a wide diversity of species, mainly through recruitment (Reid
510 *et al.*, 2001b; Stige *et al.*, 2006; Goikoetxea and Irigoien, 2013) or post-recruitment growth
511 (Ottersen *et al.*, 2001) processes.

512 Several mechanisms can explain the connection between this index and the productivity potential
513 of fish species in the Celtic Sea. The NAO is closely linked to water circulation (Hurrell and Deser,
514 2010) and notably influences the distance of the North Atlantic Subpolar Gyre to the Celtic shelf
515 (Alheit *et al.*, 2019). The inflow of Atlantic waters from the subpolar gyre to the Celtic Sea favored
516 during positive phases of the NAO is likely to influence zooplankton composition. Such inflows are
517 associated with *C. finmarchicus* advection up to the Celtic Sea (Sundby, 2000). Compared to the
518 dominant species in the Celtic Sea (*C. helgolandicus*), *C. finmarchicus* develops earlier in the year
519 (Planque and Fromentin, 1996) and has an upper position within the water column (Williams,
520 1985). Its higher abundance would possibly increase the food availability of the early spring larvae
521 of several species and improve their survival (Beaugrand *et al.*, 2003), thus explaining the positive
522 correlation observed between NAO and *C. finmarchicus*.

523 Another likely mechanism of the NAO action on productivity is the modification of local wind
524 patterns. In the Celtic Sea, winds mainly directed toward the northeast would be further directed
525 to the north when the NAO is high (similar trends in NAO and northward wind component,
526 Appendix B Fig. B.1). The resulting increase in the Ekman transport of superficial water masses to
527 the east would favor eggs and larvae retention on the shelf and larvae transport to nurseries
528 (Goikoetxea and Irigoien, 2013). The lower amplitudes of changes in sole and plaice productivity
529 potential would thus result from their higher dependence on coastal areas for coastal and nursery
530 sites (Ellis *et al.*, 2012).

531 The unfavorable conditions in the early 1960s due to the NAO shift into a strongly negative phase
532 may have accelerated the biomass decline of some species, such as hake and whiting. Conversely,
533 the favorable conditions in the 1990s caused by the strong NAO positive phase may have mitigated
534 fishing impact, preventing species from further collapse while fishing pressure culminated at that
535 time. The benefits from these conditions were likely amplified because the environment is known
536 to affect recruitment deeper for spawning biomass levels (Brander, 2005).

537 The Celtic Sea ecosystem also appeared to be influenced by global thermal conditions of the North
538 Atlantic. This effect was mainly perceived through the dynamic of pilchard productivity. In 1961,
539 contemporary to the downward shift in the AMO index and in SST, pilchard productivity potential
540 declined by 40%, leading to an abrupt decline in its biomass. After another decline in 1981, it
541 shifted upward in the early 1990s, when the AMO and SST increased. This result corroborates
542 previous studies based on long-term variability in pilchard egg numbers (Southward, 1980;
543 Southward *et al.*, 1988; Edwards *et al.*, 2013), highlighting that its productivity changes according
544 to the transition between warm and cold phases of the North Atlantic. Such dependence on
545 thermal conditions is responsible for the alternation between pilchard and herring as the dominant
546 pelagic species over time (Edwards *et al.*, 2013). However, despite the cold period from the 1960s
547 to the 1980s, which should have been favorable, herring did not show any improvement in
548 productivity potential. This result is probably linked to its overexploitation at that time (biomass
549 was divided by 6 over 1950-1960) and trophic limitation (Lauria *et al.*, 2012).

550 *4.4. A major environmental shift in the late 1980s*

551 The Celtic Sea is part of the North Atlantic Ocean and is impacted by the great hydroclimatic
552 changes that occurred at the global scale (Reid *et al.*, 2016). Hence, as observed in numerous
553 neighboring Northeast Atlantic ecosystems, the Celtic Sea experienced an ecosystem shift during
554 the 1980s (Southward, 1980; Reid *et al.*, 2001a; Mollmann *et al.*, 2008; Conversi *et al.*, 2010) . Such
555 a major change in the ecosystem was reflected in the species productivity potential values.

556 The 1980s step increase observed in the main pattern of productivity variability matched a period
557 of major changes in the environmental conditions in the Celtic Sea. The increase in wind speed, the
558 variable that was best correlated with this pattern, may have improved water mixing, hence
559 leading to an increase in primary production (Reid *et al.*, 1998; Reid and Beaugrand, 2002), which
560 was likely boosted by the dramatic increase in SST in the Celtic Sea in 1989. Thus, primary producer
561 biomass almost doubled between 1980 and 2000.

562 However, this increase in primary producer biomass did not result in a more productive ecosystem.
563 The year 1988 marked a severe decline in the abundance of small copepods, while larger copepod
564 abundance has increased since that period (Appendix B). These changes are identified as a
565 consequence of synergetic effects of multiple hydroclimatic factors (Beaugrand, 2002, 2003).

566 These changes are probably what triggered opposite trajectories in the mean productivity potential
567 between pelagic and demersal fish species. Indeed, small copepods constitute the primary food
568 source of small pelagic larvae (Checkley, 1982; Peterson and Ausubel, 1984; Last, 1989; Fernandez
569 and Gonzalez-Quiros, 2006). In contrast, larvae and young stages of large demersal fish are more
570 dependent on larger species of zooplankton (Bromley, 1997; Heath and Lough, 2007; Morote *et al.*,
571 2011). Furthermore, zooplankton abundance was probably not limiting for large demersal fish
572 production compared to pelagic species.

573 Last, independent of any trophic control, the productivity of various species could have been
574 directly driven by environmental changes, especially those related to temperature (Rijnsdorp *et al.*,
575 2009). In particular, species with the highest thermal preferenda, such as sea bass, megrim and
576 anglerfish, would be positively impacted, as established by Auber *et al.* (2015) in the adjacent
577 eastern English Channel. This change would also partly explain the growth in boarfish abundance
578 during the last decade (Coad, 2014). As suggested by trends in the catch-based Shannon index,
579 warming would also favor the settlement of Lusitanian species in the Celtic Sea, such as gurnards,
580 mullet and pouts (ter Hofstede *et al.*, 2010).

581 4.5. *First signs of recovery*

582 Over the last decade, fishing pressure in the Celtic Sea has been sharply reduced, but the mean
583 F/F_{MSY} for our studied stocks was still equal to 1.15 in 2015. In addition, this average value masks
584 the great heterogeneity among species. The exploitation rate was considerably reduced for some
585 species (e.g., $F=0.72 \cdot F_{MSY}$ for herring) but was still high for others (e.g., $F=1.3 \cdot F_{MSY}$ for sea bass),
586 and 6 species remained overexploited. The concomitance between fishing pressure reduction and
587 favorable or unfavorable environmental conditions determines the recovery dynamic: few species
588 have benefitted from higher productivity over the last 15 years (i.e., megrim, sea bass, and
589 anglerfish), but most have lower productivity than their values in the 1990s, thus recovering slowly
590 relative to the reduction in fishing effort.

591 The greatly degraded status of several historically exploited stocks and the consequent reduction in
592 their resilience capacity would also explain this slow improvement (Neubauer *et al.*, 2013). Froese
593 and Proelß (2010) were correct when predicting that the target of “phas[ing] out overfishing by
594 2015” (European Commission, 2011) would not be met. Nonetheless, slight though they may be,
595 the post-2000 trends in biomass are encouraging in terms of fisheries management (Cardinale *et*
596 *al.*, 2013; Fernandes and Cook, 2013). Additionally, all the size- and trophic-based indicators
597 calculated on catches indicated a recent improvement of the ecosystem status and structure
598 characterized by a return of larger and higher TL species. The drastic reduction in mackerel and
599 horse mackerel abundance may also lead to a progressive rebalancing between demersal and
600 pelagic compartments, highlighting similar changes as those observed in the eastern English
601 Channel (Auber *et al.*, 2015; McLean *et al.*, 2019).

602 Nonetheless, the current recovery in the last decade must be analyzed considering the historical
603 biomass levels. Species abundance and ecosystem indicators in the Celtic Sea are only reaching
604 values equivalent to those in the late 1980s, when stock biomasses were, on average, almost 3
605 times smaller than those in the year 1950, i.e., this was certainly not the beginning of the fishing

606 impacts on marine resources. However, it must be emphasized that environmental changes that
607 occurred over recent decades actually prevent any return to the state of marine ecosystems in
608 1950. Furthermore, future changes, especially those linked with ongoing climate change, must be
609 considered in fisheries management in upcoming decades.

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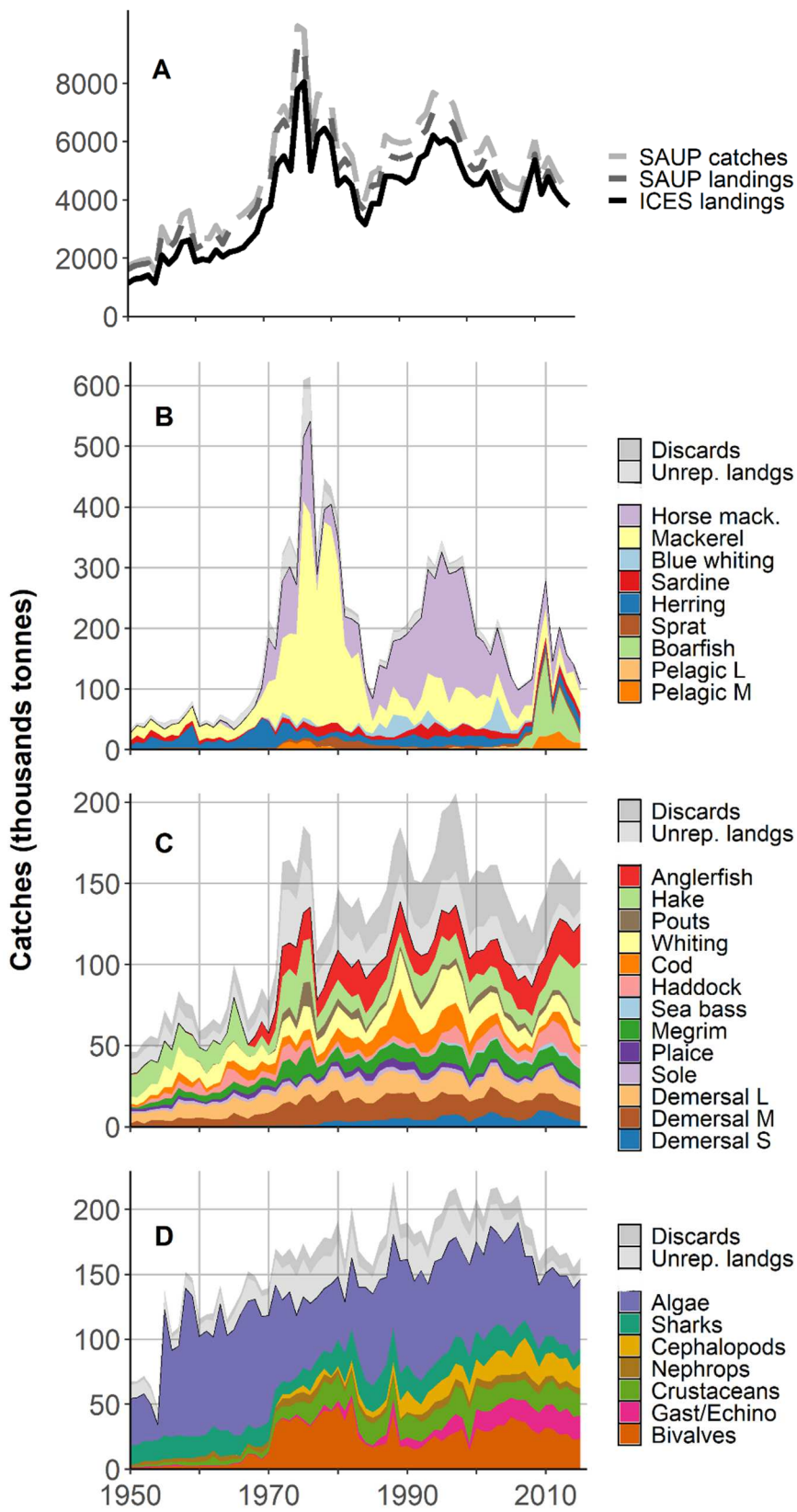
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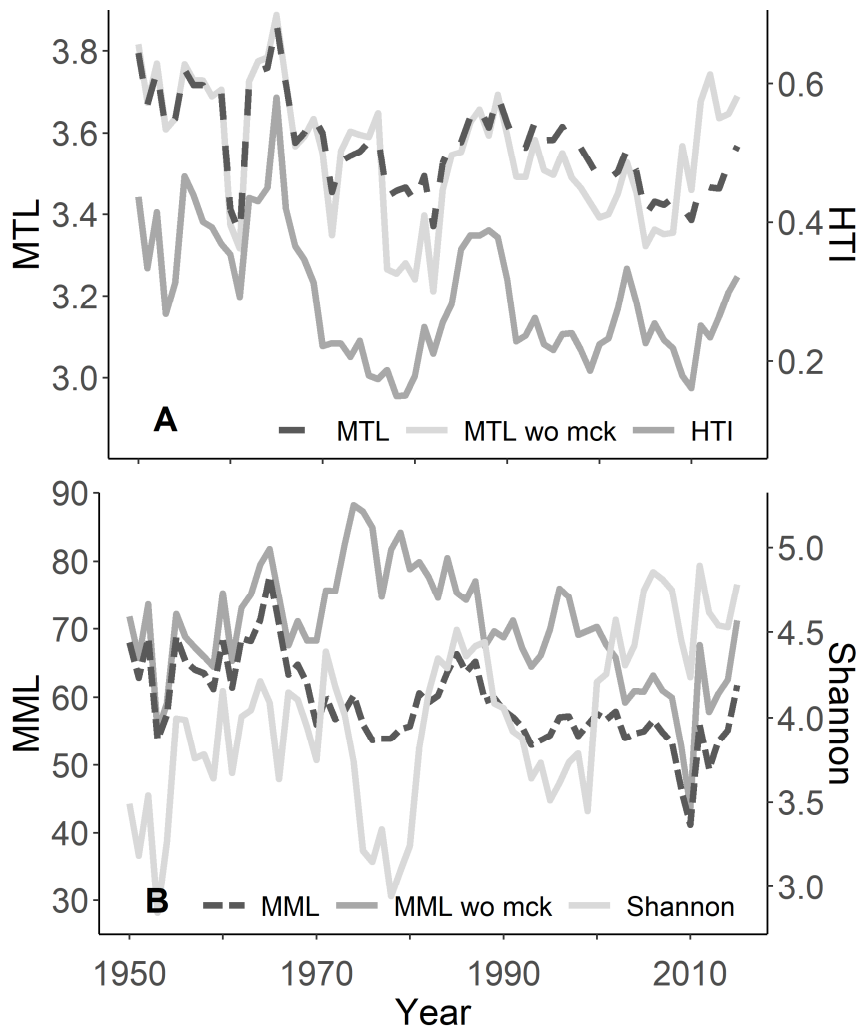
1 Figures

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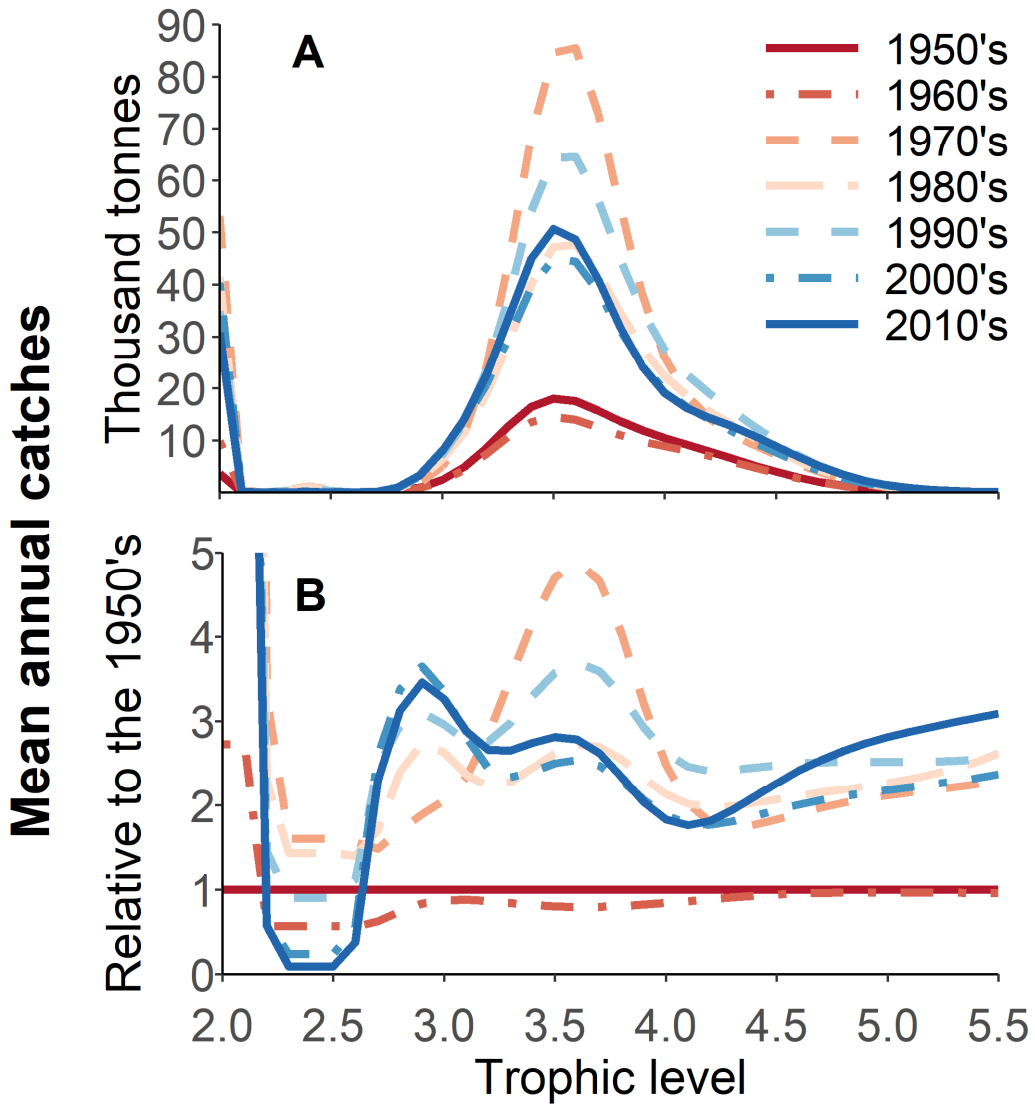
5 **Figure 1** – ICES landings and SAUP reconstructed catches in the Celtic Sea between 1950 and
6 2015: a) total catch, b) pelagic fish, c) demersal finfish, d) others. Species groups correspond to
7 Ecopath groups from Moullec et al. (2017) except in d) where they have been aggregated by
8 taxa for clarity. Unreported catches for seaweeds were not considered.



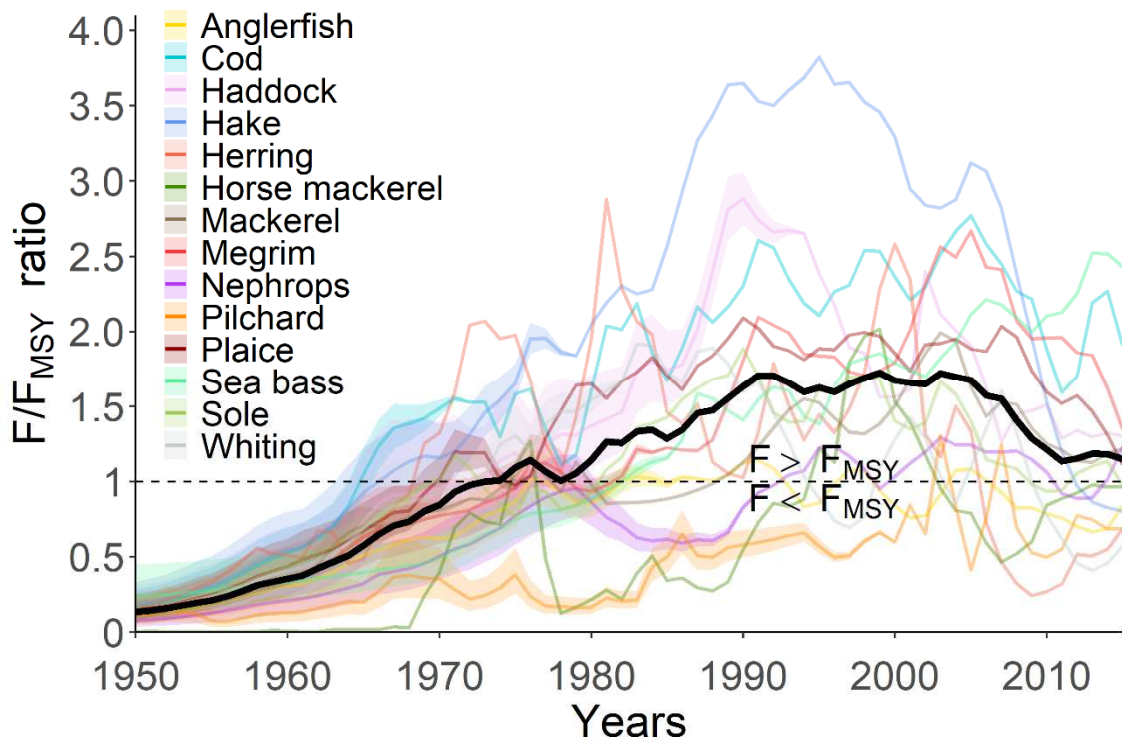
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11 **Figure 2** – Trends over the 1950-2015 period for ecosystem indicators calculated upon catch
 12 data (A) The upper panel presents two trophic indicators: mean trophic level calculated both
 13 including and excluding mackerels (MTL and MTL wo mck) and high trophic level indicator
 14 (HTI); (B) The lower panel presents size-based and species diversity indicators: the mean
 15 maximum length calculated both including and excluding mackerels (MML and MML wo mck)
 16 and the Shannon's index. Removals of primary producers are not considered in the calculation
 17 of trophic indices.

18



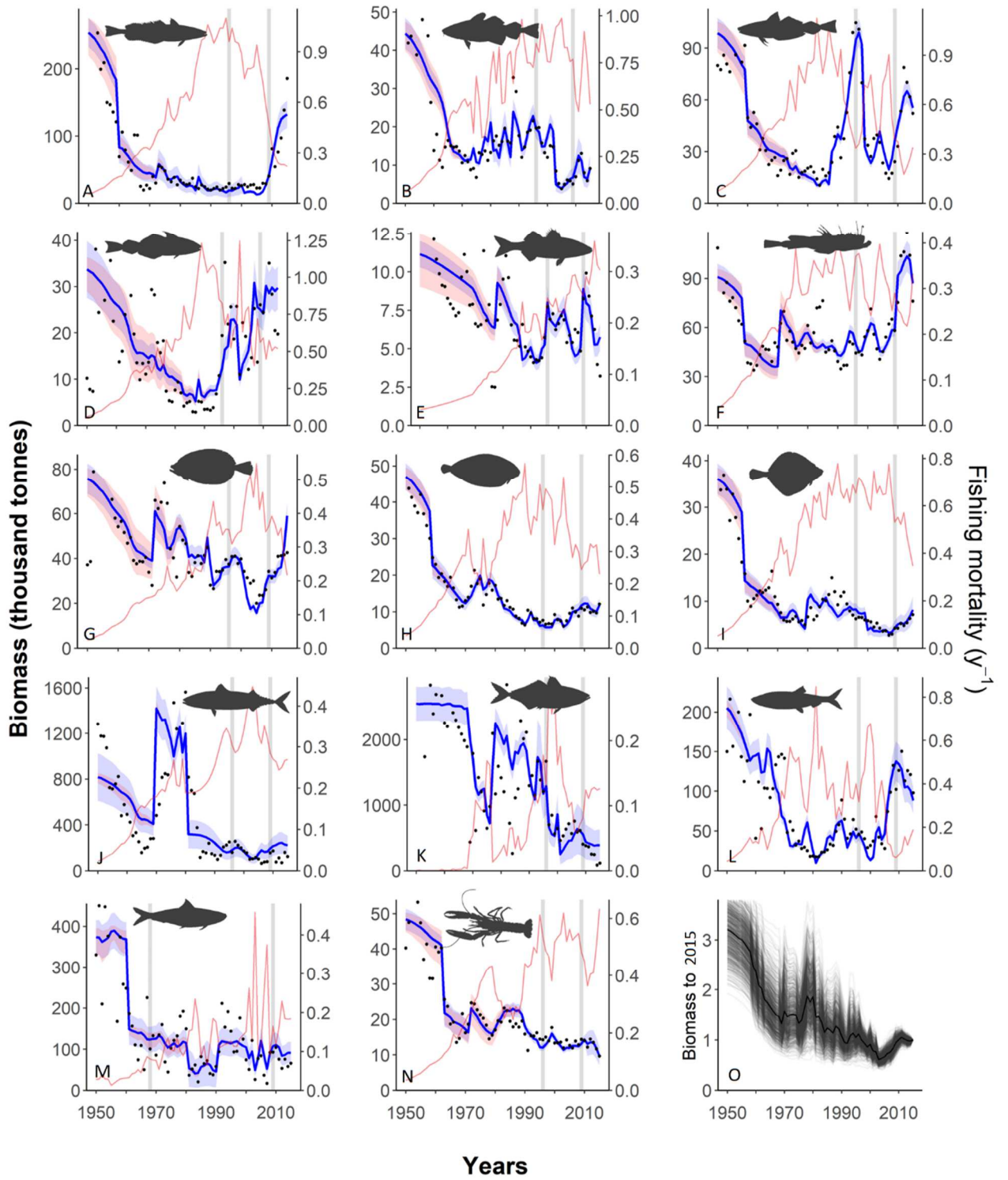
21 **Figure 3** - Decadal trophic spectra of catches (mean annual catch on the decade by trophic
 22 class of 0.1 TL wide range): (A) absolute values, (B) relative to the 1950's.



24

25 **Figure 4** - F/F_{MSY} ratio for the 14 modeled species (colors) and mean ratio (black). Lines
 26 correspond to the standard scenario regarding the fishing power increasing rate (Pauly and
 27 Palomares, 2010) and productivity (regime shifts), while the shaded area takes into account
 28 the uncertainty around this value (-50 %; +50%). The shaded area progressively recedes with
 29 time, as the number of stocks with F estimates from ICES WG increases.

30



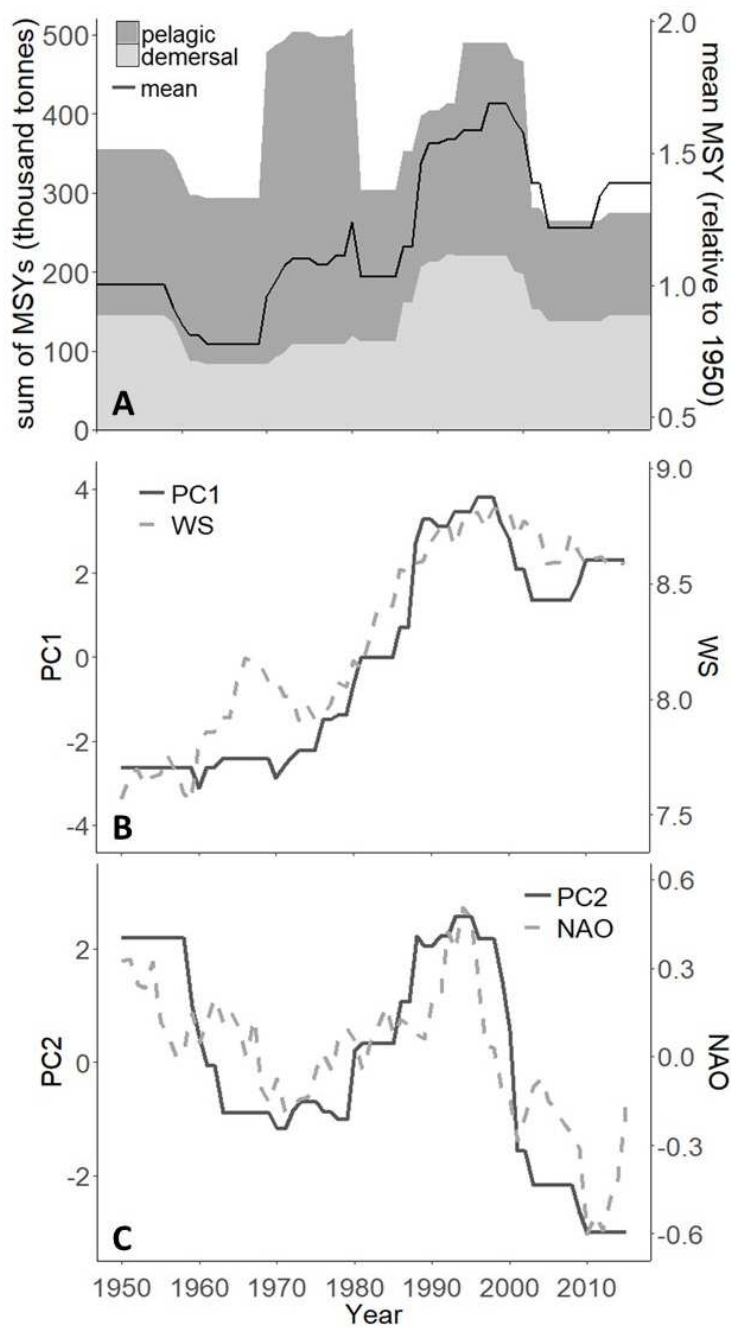
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32

33 **Figure 5** - Temporal trends in observed and estimated biomass from the surplus production
34 model applied to the 14 studies species. Vertical grey bars correspond to occurring shifts; blue
35 lines represent estimated biomass; dots correspond to the observed Y/F ratio. The blue shaded
36 areas represent the 95% confidence around the MSY value estimate. The red shaded areas
37 represent the uncertainty issued from the sensitivity analysis on the α values. The red lines are
38 the reconstituted fishing mortality series (not Fox Fishing mortality). A = hake, B = cod, C =
39 whiting, D= Haddock, E = sea bass, F = anglerfish, G = megrim, H =sole, I = plaice, J = mackerel,
40 K = horse mackerel, L = herring, M = pilchard, N = nephrops.

41 The last graph O presents the mean time-trajectory of B/B_{2015} for the 14 study-species, in
42 black, and a bootstrap within the 14 species, in grey. A

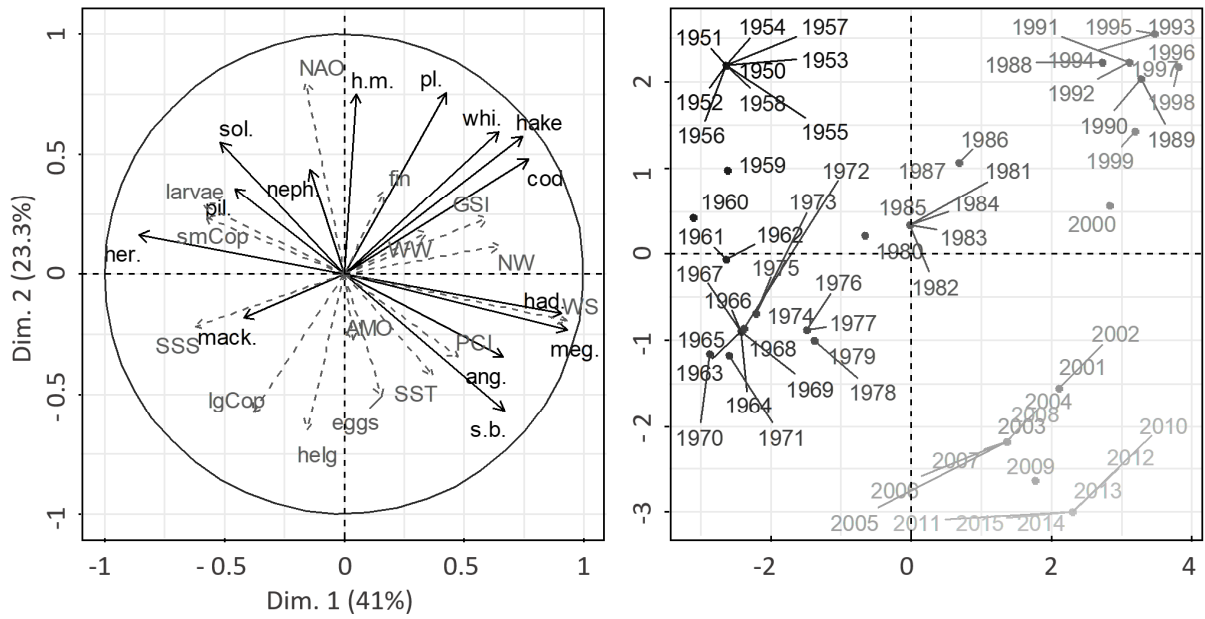
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46 **Figure 6** - Trends in species productivity potential. (A) Sum of the MSYs for pelagic (in dark
 47 grey) and demersal study species (in light grey) and mean change in productivity potential
 48 relative to 1950 among species (in black). While the first one is an index of ecosystem
 49 productivity, the second indicates the raw evolution of species productivity potential without

50 taking into account the differences in their absolute values. (B) First PC score of the PCA on
51 species productivity potential and best correlated environmental variables (C) Second PC score
52 and best correlated environmental variables.



53

54 **Figure 7** – Correlations circle (left) graph of individuals (right) of the PCA for PC1 and PC2. Black
 55 full arrows represent species productivity potentials (cod=cod, whi=whiting, hake=hake,
 56 ang.=anglerfish, meg.=megrim, had.=haddock, s.b.=sea bass, h.m.=horse mackerel,
 57 pil.=pilchard, pl.=plaice, her.=herring, mack.=mackerel), considered as active variables, and
 58 grey dotted arrows represent environmental variables (acronyms of environmental variables
 59 are defined in the text).

1 **Tables**

2

3 Table 1 – Parameters of the biomass production models and the final combinations of
 4 productivity regime shifts they include after selection according to Akaike’s scores. The
 5 selection is used Global fit quality of the model is given by the usual R^2 ; AIC is the Akaike’s
 6 coefficient of the model; AIC cst. prod. is the Akaike’s coefficient of the model based on the
 7 hypothesis of a constant productivity; corr ICES is the correlation coefficient between the
 8 predicted biomass time-series and the biomass estimates from the ICES working groups; Nb
 9 shifts is the number of shifts considered in the reference model; BPn and MSYn refer to years
 10 of shifts and values of the productivity potential MSY before that shift.

11

Name	Acronym	Type	Scale	Starting year	Potential role	Data origin/Reference
North Atlantic Oscillation	NAO	Abiotic	Global	1950	Driver of species productivity	Hurrell, 1995
Atlantic Multidecadal Oscillation	AMO			1950		Kerr, 2000
Gulf Stream Index	GSI			1966		Taylor <i>et al.</i> , 1998
Sea surface temperature	SST		1950	International Comprehensive Ocean-Atmosphere Data Set ICOADS		HadISST - MetOffice Hadley Centre
Sea surface salinity	SSS					EN4 - MetOffice Hadley Centre
Wind speed	WS					
Westard wind component	WW					
Northward wind component	NW					
Small copepod counts	SmCop					Biotic
Large copepod counts	LgCop					
Calanus finmarchicus counts	Chel					
Calanus helgolandicus counts	Cfin					
Phytoplankton colour index	PCI					
Fish eggs counts	egg					
Fish larvae counts	larv	Indicator of overall fish productivity				

12

13 Table 2 – Parameters of the species-specific biomass production models and the final
14 combinations of productivity regime shifts they include after selection according to Akaike’s
15 scores. α is the annual rate of increase in fishing efficiency calculated from Palomares et Pauly
16 (2010); AIC , AIC_{cst} , AIC_{cont} respectively correspond to AIC scores of the reference model
17 (biomass production model including shifts in productivity regimes) for the finally selected
18 combination of *MSY* regimes, and of alternative models including constant productivity and
19 continuous changes in the productivity; R^2 is the usual measure of the fit between data and
20 the reference model estimates; r_{ICES} is the correlation coefficient between the biomass time-
21 series estimated by the reference model and the biomass estimates from the ICES working
22 group

23 s ; n shifts is the number of shifts considered in the reference model; BP_n and MSY_n indicate years of shifts and the MSY values for the period preceding the shift.

	α (%)	AIC_{ref}	AIC_{cst}	AIC_{cont}	R^2	r_{ICES}	n shifts	MSY_1 (10^3t)	BP_1	MSY_2 (10^3t)	BP_2	MSY_3 (10^3t)	BP_3	MSY_4 (10^3t)	BP_4	MSY_5 (10^3t)
Hake	3.97	-1077	-1046		0.87	0.97	4	31.5	1960	14.8	1973	25.9	1986	75.3	2001	30.4
Cod	4.57	-1591	-1504		0.78	0.79	3	6.8	1980	13.6	1988	24.2	2003	7.9	-	-
Whiting	3.71	-1000	-912		0.87	0.75	3	21.8	1960	13.8	1988	37.9	1999	18.7	-	-
Haddock	3.20	-521	-503		0.37	0.51	1	5.7	1988	16.0	-	-	-	-	-	-
Sea bass	3.54	-1123	-1004		0.62	0.41	3	0.7	1978	1.0	1996	2.0	2009	3.1	-	-
Anglerfish	3.50	471	560		0.73	0.31	3	12.6	1959	8.4	1971	16.6	2010	25.0	-	-
Megrim	3.60	-927	-829		0.60	0.78	2	6.0	1972	9.7	1989	16.0	-	-	-	-
Sole	4.80	-1736	-1691		0.86	0.66	3	5.6	1959	3.5	1971	4.4	1993	3.2	-	-
Plaice	4.11	-1422	-1371		0.83	0.69	3	5.4	1959	2.8	1980	7.0	2000	3.2	-	-
Mackerel	4.47	-1007	-939		0.62	0.59	2	73.2	1970	258.3	1981	60.5	-	-	-	-
Scad	5.39	-490	-457		0.66	0.82	2	113.2	1992	190.3	2001	48.4	-	-	-	-
Herring	7.34	-1893	-1887		0.62	0.76	1	23.1	1976	16.8	-	-	-	-	-	-
Pilchard	2.98	94	155		0.71	0.95	3	40.8	1961	16.5	1981	8.8	1991	17.9	-	-
Nephrops	3.54	-727	-686		0.86	0.51	1	8.6	1963	4.7	1972	6.6	-	-	-	-

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