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## **Extending full protection inside existing multiple-use marine protected areas or reducing fishing effort outside can both deliver conservation and fisheries outcomes**

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1 **Extending full protection inside existing multiple-use marine protected**  
2 **areas or reducing fishing effort outside can both deliver conservation and**  
3 **fisheries outcomes**

4  
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26 **Running head:** Full protection helps rebuild fish stocks

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## 29 Abstract

30 1 Most fish stocks worldwide are overfished, and many fisheries management strategies  
31 have failed to achieve sustainable fishing. Identifying effective fisheries management  
32 strategies has now become urgent.

33 2 Here, we developed a spatially-explicit metapopulation model accounting for seascape  
34 connectivity in the Mediterranean Sea, and parameterized it for three ecologically and  
35 economically important coastal fish species: *Diplodus sargus*, *Diplodus vulgaris* and  
36 *Epinephelus marginatus*.

37 3 We used the model to assess how stock biomass and catches respond to changes in  
38 fishing mortality rate ( $F$ ) and in the size of fully protected areas within the existing  
39 network of multiple-use marine protected areas (MPAs). For each species, we  
40 estimated maximum sustainable yield (MSY) and the corresponding values of stock  
41 biomass ( $B_{MSY}$ ) and fishing mortality rate ( $F_{MSY}$ ), providing crucial reference points  
42 for the assessment of fisheries management.

43 4 All three species are currently overexploited. Stock recovery to  $B_{MSY}$  requires a  
44 reduction of current  $F$  between 25–50% (depending on the species). This would  
45 guarantee an increase in both stock biomass (17–42%) and catch (2–13%) after a  
46 transient time of ~10–20 years. Alternatively, increasing the size of fully protected  
47 areas over fishable areas within the existing network of MPAs would lead to positive  
48 conservation effects for all three species without impairing the productivity and  
49 profitability of the fishery.

50 5 *Synthesis and applications.* We provide the first assessment of stock status for three  
51 coastal species in the north-western Mediterranean and evaluate the ecological and  
52 fisheries outcomes of different management strategies. Extending full protection

53           inside existing multiple-use marine protected areas and or reducing fishing pressure  
54           effort outside can both deliver conservation and fisheries outcomes.

55

56   Key words

57   Fisheries management, Metapopulation models, Coastal fish, Stock assessment, Marine  
58   conservation.

## 59 **1 Introduction**

60 Marine fisheries provide a major source of food and livelihood for hundreds of millions of  
61 people worldwide (FAO 2018). However, most of the world's fish stocks are overfished  
62 (Costello *et al.* 2016), with strong cascading impacts on both marine biodiversity (Sala *et al.*  
63 2012; Ortuño Crespo & Dunn 2017) and societies (Golden *et al.* 2016).

64 Several strategies have been proposed to pursue sustainability in fisheries (Hoggarth 2006;  
65 Coll *et al.* 2013; Goetze *et al.* 2016; Carvalho *et al.* 2019). Traditional management has  
66 focused on adjusting fishing effort to levels guaranteeing maximum sustainable yield (MSY),  
67 i.e. the maximum catch that can be removed from a stock over time without depleting it. MSY  
68 and its related biological reference points, such as stock biomass ( $B_{MSY}$ ) and fishing mortality  
69 rate ( $F_{MSY}$ ), are benchmarks used for gauging the status of a stock or fisheries (Hilborn &  
70 Ovando 2014). Although many coastal species are key targets for small scale artisanal and  
71 recreational fisheries (Lloret *et al.* 2019), for most of them these reference points have never  
72 been assessed.

73 In coastal areas, multiple-use Marine Protected Areas (MPAs) can be used as a means to  
74 combine maritime spatial planning and the ecosystem approach to fisheries management  
75 (Claudet *et al.* 2006; Gaines *et al.* 2010; Melià *et al.* 2016). Their actual ecological  
76 effectiveness is affected by the presence and extent of fully protected areas within MPA  
77 borders (Zupan *et al.* 2018). Although they are often not established primarily for fisheries  
78 management (García-Charton *et al.* 2008), MPAs can provide benefits to fisheries (Russ &  
79 Alcala 2004; Di Franco *et al.* 2016) and other socioeconomic activities (Pascual *et al.* 2016).  
80 Finding a balance between biological conservation and socioeconomic viability is  
81 fundamental to ensure the consensus among stakeholders necessary for the success of MPAs  
82 (Klein *et al.* 2013; Melià 2017).

83 Whether benefits at the local scale (thanks to recruitment subsidy and/or spillover effects; Di  
84 Lorenzo *et al.* 2016) can scale-up and make MPAs useful tools for fisheries management also  
85 at a broader scale is still controversial (Hilborn 2015; Hughes *et al.* 2016). Quantitative tools  
86 able to describe the coupled spatiotemporal dynamics of fish and fisheries are hence crucial to  
87 assess the actual implications of proposed management measures in a realistic way (Botsford  
88 *et al.* 2009; Bastardie *et al.* 2017). Although studies linking seascape connectivity with  
89 population dynamics are scarce to date (but see, e.g., Watson *et al.* 2012; Treml *et al.* 2015),  
90 the explicit integration of these aspects into a metapopulation approach is key to understand  
91 the ecological and evolutionary dynamics of coastal marine populations, as well as to assess  
92 the long-term consequences of alternative management policies from a spatially explicit  
93 perspective (Botsford *et al.* 2009; Guizien *et al.* 2014).

94 Here we developed two sets of scenarios to assess the role of MPA networks as a tool to  
95 support fisheries management of three key coastal species in the north-western Mediterranean  
96 Sea. The scenarios were simulated using a biophysical metapopulation model, based on  
97 realistic patterns of connectivity estimated via Lagrangian simulations. The performances of  
98 each scenario were evaluated in terms of three indicators of conservation and socioeconomic  
99 relevance: stock biomass, fisheries catch and total value of catch. First, we tested the effects  
100 of regulating fishing mortality rates and estimated biological reference points for the three  
101 species. Second, we tested the role of the presence and size of fully protected areas in  
102 determining the bio-economic effectiveness of multiple-use MPAs. Finally, we discussed the  
103 effectiveness of the considered scenarios for achieving sustainable fisheries management  
104 objectives.

## 105 **2 Methods**

### 106 **2.1 Case study**

107 The study area covers the north-western Mediterranean Sea, and in particular the region  
108 located between latitudes 38.5°N– 45°N and longitudes 1°E–12°E. We focused on three fish  
109 species of high ecological and economic relevance (Guidetti *et al.* 2014) and vulnerable to  
110 small scale and recreational fishing (Lloret *et al.* 2019): the white seabream *Diplodus sargus*,  
111 the two-banded seabream *Diplodus vulgaris*, and the dusky grouper *Epinephelus marginatus*.  
112 The three species are common in the Mediterranean Sea: they thrive in littoral rocky bottoms  
113 and generally occur from a few meters down to approximately 50 m depth, although they can  
114 be found, at lower densities, even at greater depths (especially *E. marginatus*; Harmelin &  
115 Harmelin-Vivien 1999). Their bipartite life cycle is typical of the majority of coastal species,  
116 with a pelagic larval phase and a benthic adult phase (see section S1 in the Supplementary  
117 Information for further details).

### 118 **2.2 Metapopulation model**

119 We developed an age-structured, discrete-time metapopulation model, based on a biophysical  
120 model accounting for habitat suitability and oceanographic connectivity. The model describes,  
121 in a spatially explicit framework, all the key biological processes affecting the species'  
122 demographic dynamics, such as reproduction, larval dispersal, recruitment, and natural and  
123 fishing mortality. In the following sections, we concisely summarize the main features of the  
124 model; further details about its structure and formulation are given in section S2, while details  
125 on its calibration and validation are given in section S3.

#### 126 **2.2.1 Habitat suitability**

127 The selected fish species have very similar habitat requirements. Therefore, we assumed the  
128 same suitable habitat (rocky and hard substrate, including coralligenous assemblages between

129 0–50 m depth) for all three species. Habitat was mapped using available information on  
130 bathymetry and seabed habitats from the EMODnet portal ([www.emodnet.eu](http://www.emodnet.eu)). Bathymetry  
131 was provided as a high-resolution raster map (1/480°; Populus et al. 2017). Seabed habitat  
132 maps were hand-corrected in QGIS software; in fact, although EMODnet maps represent the  
133 most updated georeferenced seafloor maps for the Mediterranean Sea, some areas included in  
134 our domain were associated to low confidence levels, while others completely lacked any  
135 habitat information. For these areas, we first cross-checked information on the EMODnet map  
136 with the distribution of coastline substrate types reported in Furlani *et al.* (2014), and then we  
137 analysed high-resolution satellite images from Google Earth to ascertain substrate type where  
138 the information did not match. In case of mismatch or absence of habitat information in the  
139 original map, we added a buffer of rocky substrate along the coast with its extent inversely  
140 proportional to the sea bottom slope.

### 141 **2.2.2 Connectivity assessment**

142 To evaluate seascape connectivity among local populations (i.e. among model cells), we  
143 carried out Lagrangian simulations of larval dispersal across the study area with an  
144 individual-based biophysical model. The physical component of the model was based on daily  
145 average current velocity fields made available through the Copernicus Marine Environment  
146 Monitoring Service ([marine.copernicus.eu](http://marine.copernicus.eu)). Velocity fields, produced by the Mediterranean  
147 Sea physics reanalysis (Fратиanni *et al.* 2014), had a 1/16° (~6–7 km) horizontal resolution and  
148 covered 72 unevenly spaced vertical levels. Lagrangian particles were released according to  
149 the reproductive schedule of each species and tracked for the duration of the whole larval  
150 phase. Simulations covered a 12-year-long time horizon (2004–2015). Results were  
151 aggregated across a grid with the same resolution of the ocean circulation dataset (1/16°) and  
152 used to derive a set of connectivity matrices for each species and each year. The element

153  $c_{\{i,j,t\}} = \frac{n_{i \rightarrow j,t}}{n_{i,t}}$  of the connectivity matrix  $C(t)$  is the ratio between  $n_{i \rightarrow j,t}$  (i.e. the number of

154 larvae starting from source cell  $i$  and successfully arriving to destination cell  $j$  at the end of  
155 their pelagic larval duration in year  $t$ ) and  $n_{i,t}$  (i.e. the total number of propagules released  
156 from cell  $i$  in year  $t$ ). The diagonal elements of each connectivity matrix represent the  
157 retention rates of the considered cells in a specific year.

### 158 **2.2.3 Protection**

159 To describe the protection regime of each marine area, we considered three levels of  
160 protection: unprotected, partially protected and fully protected areas. Each cell within the  
161 spatial domain of the model was associated with at least one protection level. When there was  
162 more than one protection level in the same cell, we calculated the relative coverage of each  
163 protection level with respect to the total surface of the cell. To this end, we considered the 62  
164 nationally designated Marine Protected Areas (MPAs) already established in the study area.  
165 Some are fully protected areas and some are multiple-use MPAs containing a fully protected  
166 area (Horta e Costa *et al.* 2016). Partially protected areas were identified with the portion of  
167 MPA that is not fully protected. Information on the MPAs (geographical coordinates, names,  
168 areas, establishment year, presence of fully protected areas, etc.) was derived from the  
169 MAPAMED database ([medpan.org/main\\_activities/mapamed/](http://medpan.org/main_activities/mapamed/)). MPA perimeters were  
170 provided as georeferenced polygons, allowing us to define the geometric intersection with  
171 each cell and to calculate the corresponding surface area.

### 172 **2.2.4 Population dynamics**

173 Metapopulation dynamics were described by subdividing the stocks of the three species into  
174 subpopulations according to the same horizontal grid used for the connectivity assessment. To  
175 account for the heterogeneous distribution of suitable habitat within the study area, each cell  
176 was further subdivided into  $30 \times 30$  sub-cells matching the spatial resolution of the bathymetric  
177 grid. The marine surface area  $A_i$  of each cell  $i$  was evaluated as the sum of the areal extent of  
178 its sub-cells with a valid bathymetric value. For each cell  $i$ , we calculated the surface area of

179 suitable habitat  $A_i^{SH}$  as the area of the geometric intersection between the portion of cell  
180 between 0–50 m depth and the polygon of the suitable substrate. Only the cells with non-zero  
181  $A_i^{SH}$  score (949 cells in total) were included in the metapopulation model (Fig. 1). Each sub-  
182 population was subdivided into age classes (15 for *D. sargus*, 9 for *D. vulgaris* and 20 for *E.*  
183 *marginatus*), whose dynamics were described by taking into account both the local  
184 demographics and the exchange of larvae under the action of the currents.

### 185 **2.3 Fisheries management scenarios**

186 Once calibrated and validated, we used the model to test different fisheries management  
187 scenarios for the three model species at the scale of the whole study area. Specifically, we  
188 investigated the response of stock biomass and catch to changes in (i) the fishing mortality  
189 rate, and (ii) the extent of fully protected areas in the current network of MPAs. In the first set  
190 of experiments, we considered a homogeneous reduction or increase of current fishing  
191 mortality rate ( $F_0$ ) across the study area. In the second set of experiments, we changed the  
192 relative coverage of existing fully protected areas in the MPAs currently established in the  
193 study area, keeping the total surface area of each MPA unchanged. The area not included in  
194 the fully protected area was considered to be partially protected (i.e. with an intermediate  
195 level of fishing mortality).

196 For each management scenario, we performed a 50-year-long simulation with a time-averaged  
197 connectivity matrix and assuming the present distribution of the three metapopulations (as  
198 reconstructed through the calibration of the model) as the initial condition. The last ten years  
199 of each simulation were used to assess stock biomass and catch (integrated across space and  
200 averaged over time) for each species.

201 To evaluate the economic implications of the different scenarios tested, we estimated also the  
202 total value of catch (TVC) obtained from the fishery of the three study species. TVC was  
203 calculated as  $\sum_k p_k \overline{C_k}$ , where  $p_k$  is the market price of species  $k$ , and  $\overline{C_k}$  is the total catch of

204 species  $k$  averaged over the last 10 years of simulation. The relative change of TVC for each  
205 scenario was expressed as a percent change with respect to the TVC of the baseline  
206 simulation. Market prices were considered, based on an informal ex-vessel survey carried out  
207 across the study area, to be 20 EUR/kg for *D. sargus*, 18 EUR/kg for *D. vulgaris*, and 25  
208 EUR/kg for *E. marginatus*.

## 209 **3 Results**

### 210 **3.1 Effects of changing fishing mortality rate**

211 The responses of stock biomass and catch of the three studied species to changes of fishing  
212 mortality rate at the scale of the whole study area are shown in Fig. 2. To make species-  
213 specific results easier to compare, we normalized biomass and catch values for each species  
214 with respect to the baseline simulation (performed under current fishing mortality, as  
215 estimated *via* model calibration). For all three species, normalized maximum sustainable yield  
216 (MSY) and the corresponding normalized stock biomass are  $>1$ , indicating that there is room  
217 for improvement over current management. Indeed, fishing mortality rates associated with  
218 MSY ( $F_{\text{MSY}}$ ) are lower than current fishing mortality ( $F_0$ ) for all species ( $0.75F_0$  for *D.*  
219 *sargus*, and  $0.5F_0$  for *D. vulgaris* and *E. marginatus*), suggesting that all three stocks are  
220 presently overfished.

221 For *D. sargus*, baseline biomass ( $B_0$ ) and catch ( $C_0$ ) are 83% and 98% of  $B_{\text{MSY}}$  and MSY,  
222 respectively. For the other two species, the discrepancy is even more pronounced:  $B_0$  and  $C_0$   
223 for *D. vulgaris* are 64% and 90% of those associated with  $F_{\text{MSY}}$ , while for *E. marginatus* they  
224 are 58% and 87%, respectively. The relative values of  $B_{\text{MSY}}$  compared to unfished biomasses  
225 (i.e. with fishing effort set to zero across the whole study area) are 41% (for *D. sargus*), 47%  
226 (for *D. vulgaris*) and 37% (for *E. marginatus*). In parallel, the ratio of baseline biomass ( $B_0$ )  
227 on unfished biomass is 34% for *D. sargus*, 30% for *D. vulgaris*, and 22% for *E. marginatus*.

228 Fig. 3A shows the temporal dynamics of stock biomass over time under an MSY scenario. At  
229 the beginning of the simulations, relative biomass  $B/B_{MSY}$  is 0.85 for *D. sargus*, 0.61 for *D.*  
230 *vulgaris* and 0.60 for *E. marginatus*. Subsequently, relative biomass grows progressively until  
231 reaching its maximum ( $B/B_{MSY} = 1$ ). The duration of the transient required to approach  $B_{MSY}$   
232 (i.e. for a full recovery of the stock) is ~10–20 years for the three species. Fig. 3B shows the  
233 temporal dynamics of catch (expressed, in this case, as the ratio between current catch and its  
234 present value,  $C/C_0$ ) under the same scenario (MSY). Relative catches fall, during the first  
235 year of implementation of the scenario, from the present level (= 1 by definition) to  
236 approximately 0.79 for *D. sargus*, 0.55 for *D. vulgaris* and 0.54 for *E. marginatus*.  
237 Afterwards, they grow over time until reaching their maximum value (1.02 for *D. sargus*,  
238 1.11 for *D. vulgaris* and 1.15 for *E. marginatus*). The time required to attain the present levels  
239 again ( $C/C_0 = 1$ ) is about 16 years for *D. sargus*, 11 years for *D. vulgaris* and 10 years for *E.*  
240 *marginatus*.

### 241 **3.2 Effects of expanding fully protected areas**

242 Predicted responses of stock biomass and catch of the three species to changes in the relative  
243 coverage of fully protected areas (keeping fishing mortality rate at its present level  $F_0$ ) are  
244 shown in Fig. 4. The effect of expanding fully protected areas on fish biomass are positive for  
245 all species and approximately proportional to the extent of full protection. When the relative  
246 coverage of full protection is set to 100% of the total protected area, the predicted increase in  
247 stock biomass relative to the baseline is 33% for *D. sargus*, 40% for *D. vulgaris*, and 61% for  
248 *E. marginatus*. On the other hand, effects on catch are species-dependent. For *D. sargus* and  
249 *E. marginatus*, catch is negatively related to the fully protected fraction (except when this  
250 ranges between its current value and 10% of the total protected area). In contrast, for *D.*  
251 *vulgaris* the effect of increasing the fully protected fraction is generally positive, except when  
252 the fraction is lower than the present one or >90% of the total protected area. In particular,

253 catch of *D. vulgaris* is expected to be maximized by a fully protected area ~40% of the total  
254 protected area.

### 255 **3.3 Economic consequences of the analysed scenarios**

256 The response of total value of catch to changes in fishing mortality is shown in Fig. 5A.  
257 Under the current protection scheme, the predicted change in the total value of catch is  
258 positive for  $F$  comprised between  $0.4F_0$  and  $F_0$ . The maximum value (+8%) is achieved for a  
259 fishing mortality ~60% of the present one. Beyond its maximum, total value declines  
260 progressively with increasing fishing mortalities.

261 The effect of changing the extent of full protection within existing MPAs on the total value of  
262 catch are shown in Fig. 5B. The maximum value (+0.5%) is achieved when the fraction of  
263 fully protected area is equal to 20%. Benefits are positive when the fraction ranges between  
264 the current value (8%) and 30%, and become negative outside this interval.

## 265 **4 Discussion**

266 We showed that the stocks of the three studied fish species (*Diplodus sargus*, *D. vulgaris* and  
267 *Epinephelus marginatus*) are currently overexploited in the north-western Mediterranean, and  
268 that fisheries sustainability could be reached either by reducing significantly fishing mortality  
269 in unprotected areas or by increasing the size of fully protected areas while keeping fishing  
270 constant.

271 Estimated current stock biomasses ( $B_0$ ) are lower than  $B_{MSY}$  for the three studied species.  
272 However, the level of depletion ( $B_0 > 0.5B_{MSY}$  for all species) is such that all three species, and  
273 in particular *D. sargus*, have a good chance of recovery and avoid collapse if fishing pressure  
274 is reduced rapidly and substantially (Neubauer *et al.* 2013).

275 Achieving MSY requires that fishing mortality rates be significantly reduced (by one quarter  
276 for *D. sargus* and one half for *D. vulgaris* and *E. marginatus*). In practice, this could be

277 achieved through a range of management tools including both input (e.g. gear restrictions,  
278 reduction of fishing capacity) and output controls (e.g. reduction in allowable catch).  
279 Additionally, we show that in the medium/long term (10–20 years), such a prospect of fishery  
280 recovery would simultaneously generate increases in stock biomass (17–42% depending upon  
281 species), fisheries catch (2–13%) and, consequently, revenues for the fishery sector (8% of  
282 increase in the total value of catch).

283 While the positive effects on stock biomass of the three studied species would be visible  
284 immediately after starting the recovery plan, our simulations suggest that the process of  
285 rebuilding catch to levels at least equal to the current ones would take more time (16 years for  
286 *D. sargus*, 11 years for *D. vulgaris* and 10 years for *E. marginatus*). During this relatively  
287 long transient period, catches may be substantially reduced, especially in the first year (about  
288 –20% for *D. sargus* and –45% for *D. vulgaris* and *E. marginatus*). To avoid excessive  
289 socioeconomic impacts (Worm *et al.* 2009) or unreported or illegal fishing (Agnew *et al.*  
290 2009), specific measures should be targeted towards fishers during this transient period.

291 Enforcement of fishing effort control in unprotected areas may be difficult to put into  
292 practice, especially in the case of small scale and recreational fisheries in coastal areas.  
293 Therefore, an effective alternative strategy could be to rely on already designated MPAs and  
294 extend the coverage of full protection within the existing MPA network. Increasing the  
295 relative size of fully protected areas within multiple-use MPAs, while keeping fishing  
296 mortality rate outside MPAs at current levels, can generate positive conservation effects  
297 (increase in stock biomass) for the three coastal species. Positive effects of the size of fully  
298 protected areas on fish biomass are known (Claudet *et al.* 2008) and can be related to better  
299 inclusion of fish home ranges (Di Franco *et al.* 2018) and increase in self-recruitment through  
300 larger proportions of retained larvae (Botsford, Micheli & Hastings 2003).

301 Benefits on catch are species-specific and dependent on the size of the fully protected area. In  
302 our case, they are greater for the species with the longest dispersal distance (*D. vulgaris*) than  
303 for those with a narrower dispersion range (*D. sargus* and *E. marginatus*). Given that the three  
304 studied coastal species have limited adult movement (La Mesa *et al.* 2011; Di Franco *et al.*  
305 2018), the relatively short pelagic larval phase represents the primary opportunity for  
306 dispersal and connectivity (Di Franco *et al.* 2012; Andrello *et al.* 2013; Pujolar *et al.* 2013).  
307 Ensuring that the loss in fishing grounds is offset by gains in catch (Halpern & Warner 2003;  
308 Gaines *et al.* 2010) is key for successful fisheries management with MPAs. Here, we showed  
309 that an increase of size of fully protected areas within existing multiple-use MPAs can  
310 generate positive effects for *D. sargus* and *D. vulgaris*, both in terms of stock biomass (+2%  
311 and +15%, respectively) and catch (+0.5% and +4%, respectively), for levels of full  
312 protection between 10% and 40%, respectively, of the total protected area. In the case of *E.*  
313 *marginatus*, increasing the relative size of the fully protected area would not generate positive  
314 effects on catch. However, given that adult spillover was not taken into account in this study,  
315 the actual benefits on catch may be underestimated. In any case, the economic viability of the  
316 fishery (expressed in terms of total value of catch) would be preserved.

317 Despite the ecological and commercial interests of the studied coastal species, to our  
318 knowledge our study is the first modelling effort of its kind, fully integrating the biological  
319 and demographic characteristics of the species into a single model. We have shown that  
320 strong conservation benefits can be obtained either through non-spatial regulations, by  
321 reducing fishing effort in unprotected areas, or via area-based management strategies, by  
322 increasing the size of fully protected areas within existing MPAs (hence not increasing the  
323 size of MPAs overall). We believe this can contribute greatly to more effective management  
324 of those vulnerable species and help reconcile conservation and fisheries goals (Halpern *et al.*  
325 2010).

326

### 327 **Authors' contributions**

328 PM and MB conceived the ideas and designed methodology. MB developed and ran the  
329 models, with support from PM, LM, MG and RC. ADF, AC and PG contributed in  
330 acquisition and interpretation of data. MB led the writing of the manuscript. All authors  
331 contributed critically to the drafts and gave final approval for publication.

332

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340

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494 **Figure legends**

495 **Figure 1.** Study area and spatial distribution of suitable habitat in each of the 949 model cells  
496 considered in this study.

497  
498 **Figure 2.** Stock biomass and catch of the three studied species (colour coded) as functions of  
499 fishing mortality rate  $F$ . Biomass and catch values (averaged over the last 10 years of a 50-  
500 years simulation) are normalized with respect to baseline values for each species (obtained at  
501 current fishing mortality rate,  $F_0$ ).  $F$  was varied by applying different multipliers to the  
502 baseline, namely: 0, 0.1, 0.2, 0.25, 0.33, 0.5, 0.625, 0.75, 1, 1.5, 2, 3, 4, and 5. Maximum  
503 Sustainable Yield for each species and the corresponding values of stock biomass ( $B_{MSY}$ ) are  
504 pointed out by coloured dots near the axes, while the corresponding levels of fishing mortality  
505 ( $F_{MSY}$ ) are indicated by black-bordered circles. The white, black-bordered circle identifies the  
506 baseline scenario.

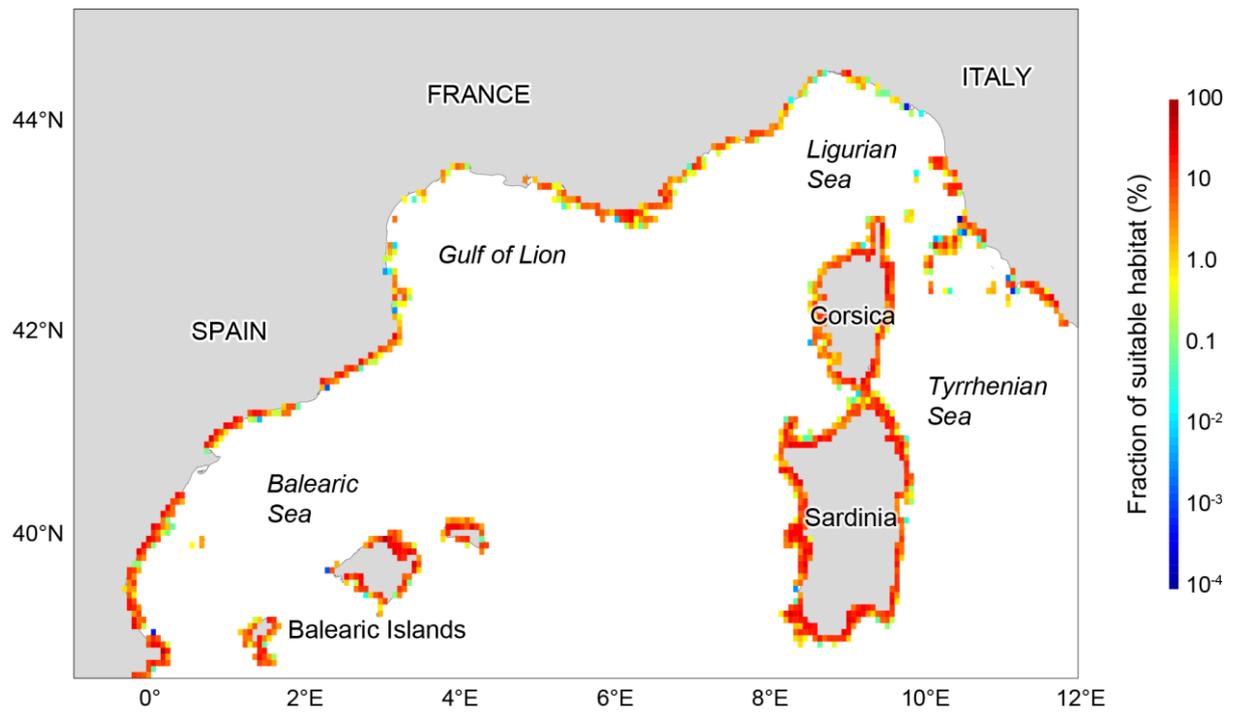
507  
508 **Figure 3.** Temporal dynamics of (A) stock biomass and (B) catch for the three studied species  
509 under a MSY management (i.e., with fishing mortality rate set to  $F_{MSY}$ ). Biomasses are  
510 normalized with respect to  $B_{MSY}$ , while catches are normalized with respect to their estimated  
511 current value  $C_0$ .

512  
513 **Figure 4.** Stock biomass and catch of the three studied species as functions of the percent  
514 coverage of fully protected areas within existing MPAs. Biomass and catch values (averaged  
515 over the last 10 years of a 50-years simulation) are normalized with respect to baseline values  
516 for each species (obtained by setting the proportion of fully protected areas over the overall  
517 size of MPAs to its present value,  $A_0$ ). The white, black-bordered circle identifies the baseline  
518 scenario.

519

520 **Figure 5.** Percent change of the total value of catch (compared to its present value) as a  
521 function of (A) fishing mortality rate and (B) percent coverage of fully protected areas within  
522 existing MPAs.

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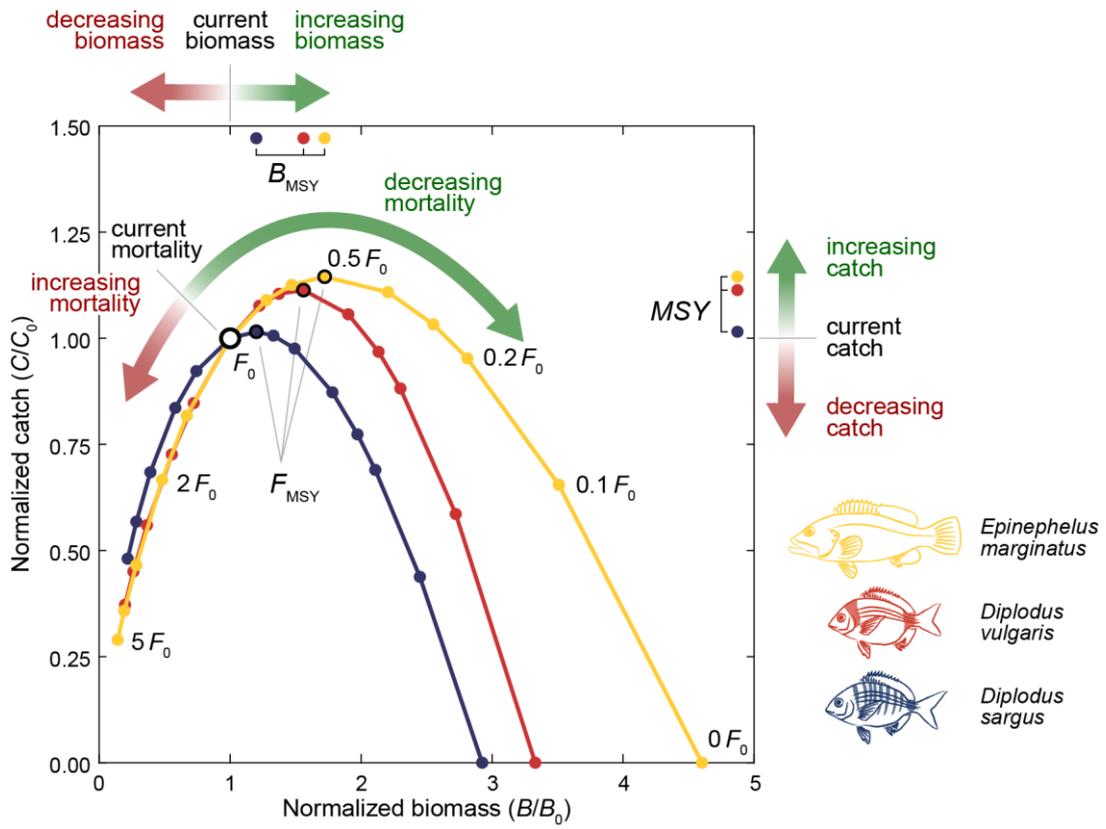


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**Fig. 1**

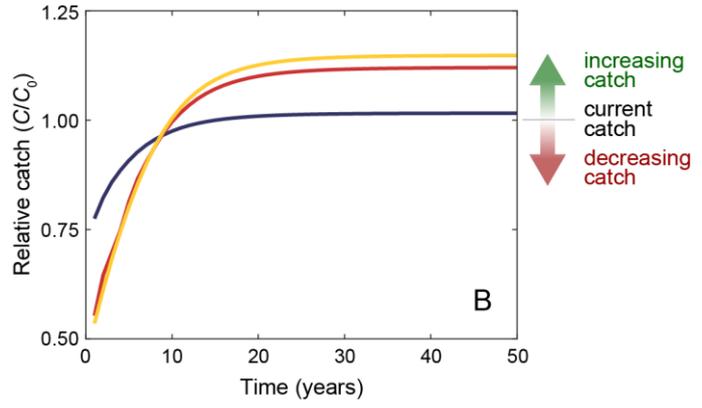
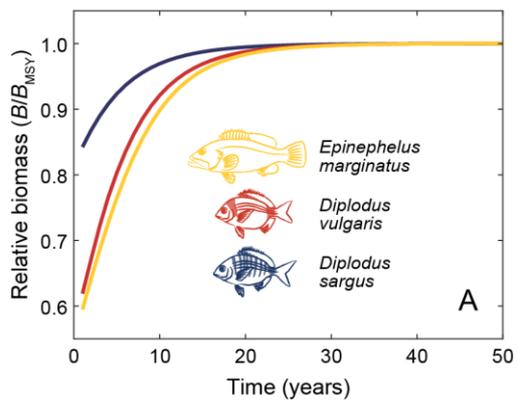


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Fig. 2

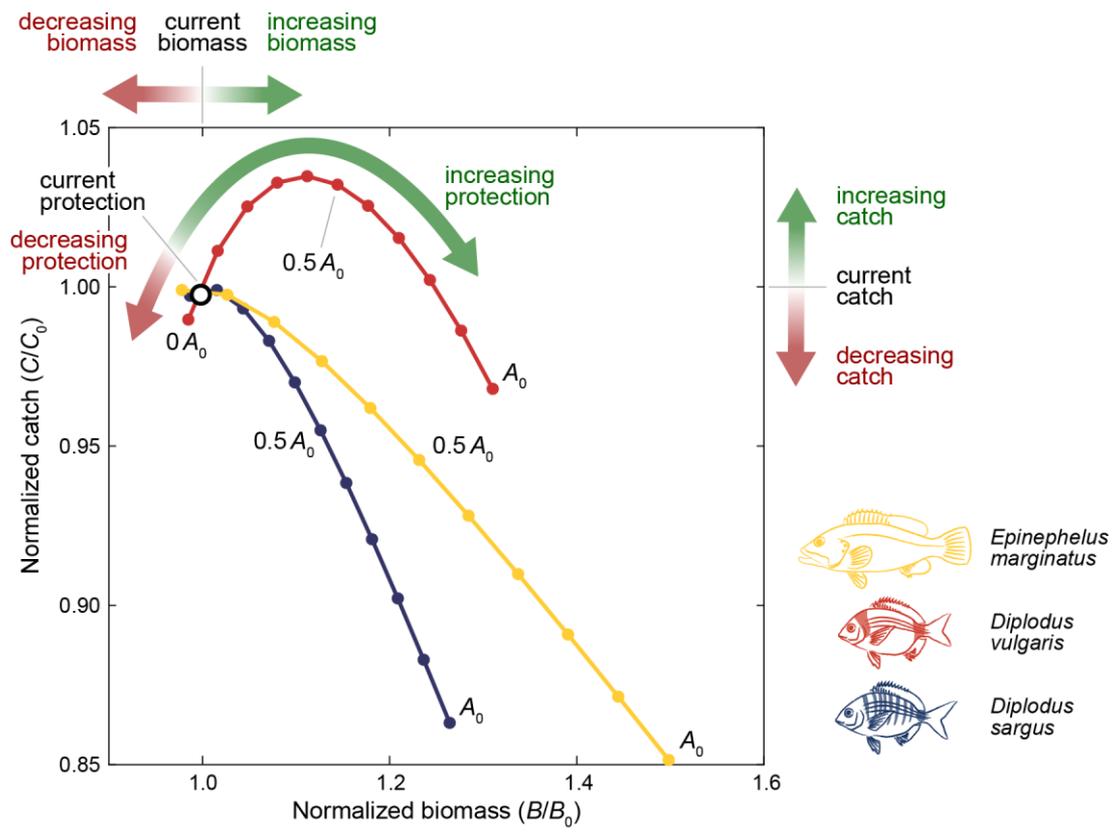


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**Fig. 3**

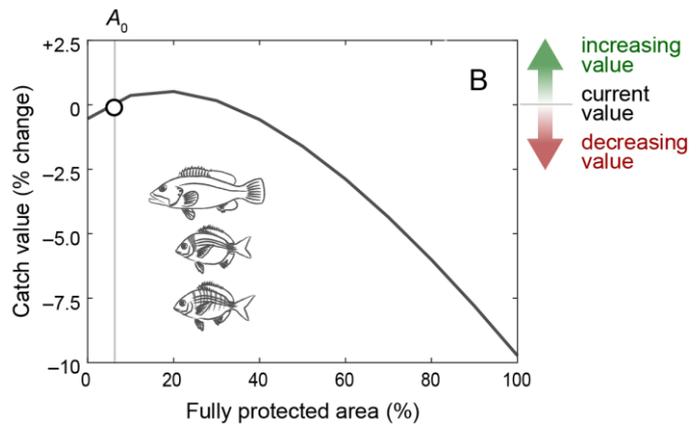
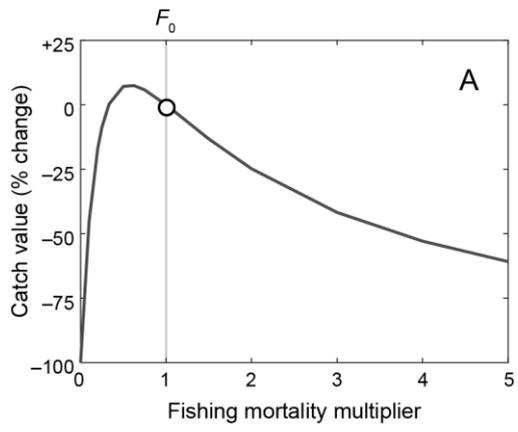


**Fig. 4**

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**Fig. 5**