



HAL
open science

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

Mokrane Belharet, Antonio Di Franco, Antonio Calò, Lorenzo Mari, Joachim Claudet, Renato Casagrandi, Marino Gatto, Josep Lloret, Charlotte Sève, Paolo Guidetti, et al.

► To cite this version:

Mokrane Belharet, Antonio Di Franco, Antonio Calò, Lorenzo Mari, Joachim Claudet, et al.. Extending full protection inside existing multiple-use marine protected areas or reducing fishing effort outside can both deliver conservation and fisheries outcomes. *Journal of Applied Ecology*, 2020, 57 (10), pp.1948-1957. 10.1111/1365-2664.13688 . hal-03034216

HAL Id: hal-03034216

<https://hal.science/hal-03034216v1>

Submitted on 1 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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
5 Mokrane Belharet¹, Antonio Di Franco^{2,3}, Antonio Calò^{2,4,5}, Lorenzo Mari¹, Joachim
6 Claudet⁶, Renato Casagrandi¹, Marino Gatto¹, Josep Lloret⁷, Charlotte Sève⁶, Paolo Guidetti²,
7 Paco Melià¹

8
9 ¹Dipartimento di Elettronica, Informazione e Bioingegneria, Politecnico di Milano, Via Ponzio 34/5, 20133
10 Milano, Italy.

11 ²Université Côte d'Azur, CNRS, UMR 7035 ECOSEAS, Parc Valrose 28, Avenue Valrose, 06108 Nice, France.

12 ³Stazione Zoologica "Anton Dohrn" sede interdipartimentale di Palermo, Italy

13 ⁴CoNISMa, Piazzale Flaminio 9, 00196 Roma, Italy.

14 ⁵Dipartimento di Scienze della Terra e del Mare (DiSTeM), Università di Palermo, Via Archirafi 20, 90123
15 Palermo, Italy

16 ⁶National Center for Scientific Research, PSL Université Paris, CRIOBE, USR3278 CNRS-EPHE-UPVD,
17 Maison des Océans, 195 rue Saint-Jacques 75005 Paris, France.

18 ⁷University of Girona, Faculty of Science, C/Maria Aurèlia Company 69, 17003 Girona, Catalonia, Spain.

19
20 **Correspondence**

21 Mokrane Belharet

22 E-mail: mokrane.belharet@gmail.com

23 Paco Melià

24 E-mail: paco.melia@polimi.it

25
26 **Running head:** Full protection helps rebuild fish stocks

27 Word count: 6523 (summary: 271; main text: 3546; acknowledgements: 66; references: 2139; figure
28 legends: 301); tables: 0; figures: 5; references: 61

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). 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). 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/). 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 30×30 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_{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_{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_{MSY} , while for *E. marginatus* they
224 are 58% and 87%, respectively. The relative values of B_{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

333 **Acknowledgements**

334 The present work has been carried out in the framework of the SafeNet project, funded by the
335 European Commission, Directorate General for Maritime Affairs and Fisheries (grant
336 SI2.721708 "Marine protected areas: network(s) for enhancement of sustainable fisheries in
337 EU Mediterranean waters" (MARE/2014/41)). Additional funding came from the European
338 Union's Horizon 2020 research and innovation programme (grant 641762
339 "ECOPOTENTIAL: Improving future ecosystem benefits through Earth observations").

340

341 **References**

- 342 Agnew, D.J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J.R. & Pitcher,
343 T.J. (2009) Estimating the worldwide extent of illegal fishing. *Plos One*, **4**, e4570.
- 344 Andrello, M., Mouillot, D., Beuvier, J., Albouy, C., Thuiller, W. & Manel, S. (2013) Low
345 connectivity between Mediterranean marine protected areas: a biophysical modeling
346 approach for the dusky grouper *Epinephelus marginatus*. *Plos One*, **8**, e68564.
- 347 Bastardie, F., Angelini, S., Bolognini, L., Fuga, F., Manfredi, C., Martinelli, M., Nielsen, J.R.,
348 Santojanni, A., Scarcella, G. & Grati, F. (2017). Spatial planning for fisheries in the
349 Northern Adriatic: working toward viable and sustainable fishing. *Ecosphere*, **8**, e01696.
- 350 Botsford, L.W., Micheli, F. & Hastings, A. (2003) Principles for the design of marine
351 reserves. *Ecological Applications*, **13**, 25–31.
- 352 Botsford, L.W., White, J.W., Coffroth, M.-A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold,
353 S.R. & Jones, G.P. (2009) Connectivity and resilience of coral reef metapopulations in
354 marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*, **28**,
355 327–337.
- 356 Carvalho, P.G., Jupiter, S.D., Januchowski-Hartley, F.A., Goetze, J., Claudet, J., Weeks, R.,
357 Humphries, A., White, C. (2019). Optimized fishing through periodically harvested
358 closures. *Journal of Applied Ecology* (in press).
- 359 Claudet, J., Osenberg, C.W., Benedetti- Cecchi, L., Domenici, P., García- Charton, J.,
360 Pérez- Ruzafa, Á., Badalamenti, F., Bayle- Sempere, J., Brito, A. & Bulleri, F. (2008)
361 Marine reserves: size and age do matter. *Ecology letters*, **11**, 481–489.
- 362 Claudet, J., Roussel, S., Pelletier, D. & Rey-Valette, H. (2006) Spatial management of near
363 shore coastal areas: The use of Marine Protected Areas (MPAs) in a fisheries management
364 context. *Life and Environment*, **56**, 301–305.
- 365 Coll, M., Cury, P., Azzurro, E., Bariche, M., Bayadas, G., Bellido, J.M., Chaboud, C.,
366 Claudet, J., El-Sayed, A.F., Gascuel, D., Knittweis, L., Pipitone, C., Samuel-Rhoads, Y.,
367 Taleb, S., Tudela, S. & Valls, A. (2013). The scientific strategy needed to promote a
368 regional ecosystem-based approach to fisheries in the Mediterranean and Black Seas.
369 *Reviews in Fish Biology and Fisheries*, **23**, 415–434.
- 370 Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch,
371 T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B., Rader, D.N. & Leland, A. (2016) Global
372 fishery prospects under contrasting management regimes. *Proceedings of the National
373 Academy of Sciences*, **113**, 5125–5129.
- 374 Di Franco, A., Coppini, G., Pujolar, J.M., De Leo, G.A., Gatto, M., Lyubartsev, V., Melià, P.,
375 Zane, L. & Guidetti, P. (2012) Assessing Dispersal Patterns of Fish Propagules from an
376 effective Mediterranean Marine Protected Area. *Plos One*, **7**, e52108.
- 377 Di Franco, A., Plass-Johnson, J.G., Di Lorenzo, M., Meola, B., Claudet, J., Gaines, S.D.,
378 García-Charton, J.A., Giakoumi, S., Grorud-Colvert, K., Hackrad, C.W., Micheli, F. &

- 379 Guidetti, P. (2018) Linking home ranges to protected area size: The case study of the
380 Mediterranean Sea. *Biological Conservation*, **221**, 175–181.
- 381 Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N.L., Jeudy
382 de Grissac, A., Koutsoubas, D., Milazzo, M., Otero, M. del M., Piante, C., Plass-Johnson,
383 J., Sainz-Trapaga, S., Santarossa, L., Tudela, S. & Guidetti, P. (2016) Five key attributes
384 can increase marine protected areas performance for small-scale fisheries management.
385 *Scientific Reports*, **6**, 38135.
- 386 Di Lorenzo, M., Claudet, J. & Guidetti, P. (2016) Spillover from marine protected areas to
387 adjacent fisheries has an ecological and a fishery component. *Journal for Nature
388 Conservation*, **32**, 62–66.
- 389 FAO (2018) *The State of World Fisheries and Aquaculture 2018. Meeting the sustainable
390 development goals*. FAO, Rome.
- 391 Fратиanni, C., Simoncelli, S., Pinardi, N., Cherchi, A., Grandi, A. & Dobricic, S. (2015).
392 "Mediterranean RR 1955-2015 (Version 1) ". [Data set]. Copernicus Monitoring
393 Environment Marine Service (CMEMS).
- 394 Furlani, S., Pappalardo, M., Gómez-Pujol, L. & Chelli, A. The rock coast of the
395 Mediterranean and Black sea. *Geological Society, London, Memoirs*, **40**, 89–123.
- 396 Gaines, S.D., White, C., Carr, M.H. & Palumbi, S.R. (2010) Designing marine reserve
397 networks for both conservation and fisheries management. *Proceedings of the National
398 Academy of Sciences*, **107**, 18286–18293.
- 399 García-Charton, J.-A., Pérez-Ruzafa, Á., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-
400 Cecchi, L., Falcón, J.M., Milazzo, M., Schembri, P.J., Stobart, B., Vandeperre, F., Brito,
401 A., Chemello, R., Dimech, M., Domenici, P., Guala, I., Le Diréach, L., Maggi, E. &
402 Planes, S. (2008). Effectiveness of European Atlanto-Mediterranean MPAs: do they
403 accomplish the expected effects on populations, communities and ecosystems? *Journal for
404 Nature Conservation*, **16**, 193–221.
- 405 Goetze, J., Langlois, T., Claudet, J., Januchowski-Hartley, F., Jupiter, SD. (2016).
406 Periodically harvested closures require full protection of vulnerable species and longer
407 closure periods. *Biological Conservation*, **203**, 67–74.
- 408 Golden, C.D., Allison, E.H., Cheung, W.W.L., Dey, M.M., Halpern, B.S., McCauley, D.J.,
409 Smith, M., Vaitla, B., Zeller, D. & Myers S.S. (2016) Nutrition: Fall in fish catch threatens
410 human health. *Nature*, **534**, 317–320.
- 411 Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F.,
412 Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M. & Sala, E. (2014) Large-Scale
413 Assessment of Mediterranean Marine Protected Areas Effects on Fish Assemblages. *Plos
414 One*, **9**, e91841.
- 415 Guizien, K., Belharet, M., Moritz, C. & Guarini, J.M. (2014) Vulnerability of marine benthic
416 metapopulations: implications of spatially structured connectivity for conservation practice
417 in the Gulf of Lions (NW Mediterranean Sea). *Diversity and Distributions*, **20**, 1392–1402.

- 418 Halpern, B.S. & Warner, R.R. (2003) Review Paper. Matching marine reserve design to
419 reserve objectives. *Proceedings of the Royal Society of London. Series B: Biological*
420 *Sciences*, **270**, 1871–1878.
- 421 Halpern, B.S., Lester, S.E. & McLeod, K.L. (2010) Placing marine protected areas onto the
422 ecosystem-based management seascape. *Proceedings of the National Academy of Sciences*,
423 **107**, 18314–18317.
- 424 Harmelin, J.-G. & Harmelin-Vivien, M. (1999) A review on habitat, diet and growth of the
425 dusky grouper *Epinephelus marginatus* (Lowe, 1834). *Marine Life*, **9**, 11–20.
- 426 Hilborn, R. & Ovando, D. (2014) Reflections on the success of traditional fisheries
427 management. *ICES Journal of Marine Science*, **71**, 1040–1046.
- 428 Hilborn, R. (2015) Marine Protected Areas miss the boat. *Science*, **350**, 1326.
- 429 Hoggarth, D.D. (ed). (2006) *Stock Assessment for Fishery Management: A Framework Guide*
430 *to the Stock Assessment Tools of the Fisheries Management Science Programme*. Food and
431 Agriculture Organization of the United Nations, Rome.
- 432 Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A., Gonçalves, E.J. (2016) A
433 Regulation-Based Classification System for Marine Protected Areas (MPAs). *Marine*
434 *Policy*, **72**, 192–198.
- 435 Hughes, T.P., Cameron, D.S., Chin, A., Connolly, S.R., Day, J.C., Jones, G.P., McCook, L.,
436 McGinnity, P., Mumby, P.J., Pears, R.J., Pressey, R.L., Russ, G.R., Tanzer, J., Tobin, A. &
437 Young, M. a. L. (2016) A critique of claims for negative impacts of Marine Protected
438 Areas on fisheries. *Ecological Applications*, **26**, 637–641.
- 439 Klein, C.J., Tulloch, V.J., Halpern, B.S., Selkoe, K.A., Watts, M.E., Steinback, C., Scholz, A.
440 & Possingham, H. (2013) Tradeoffs in marine reserve design: habitat condition,
441 representation, and socioeconomic costs. *Conservation Letters*, **6**, 324–332.
- 442 La Mesa, G., Molinari, A., Bava, S., Finoia, M.G., Cattaneo-Vietti, R. & Tunesi, L. (2011)
443 Gradients of abundance of sea breams across the boundaries of a Mediterranean marine
444 protected area. *Fisheries Research*, **111**, 24–30.
- 445 Lloret, J., Biton-Porsmoguer, S., Carreño, A., Di Franco, A., Sahyoun, R., Melià, P., Claudet,
446 J., Sève, C., Ligas, A., Belharet, M., Calò, A., Carbonara, P., Coll, M., Corrales, X.,
447 Lembo, G., Sartor, P., Bitetto, I., Vilas, D., Piroddi, C., Prato, G., Charbonnel, E., Bretton,
448 O., Hartmann, V., Prats, L. & Font, T. (2019) Recreational and small-scale fisheries may
449 pose a threat to vulnerable species in coastal and offshore waters of the western
450 Mediterranean. *ICES Journal of Marine Science* (in press).
- 451 Melià, P. (2017) Multi-criteria Decision Making for Marine Protected Area Design and
452 Management. Pp. 125-144 in Goriup P.D. (ed.) *Management of Marine Protected Areas. A*
453 *Network Perspective from the Mediterranean and Black Seas*. John Wiley & Sons, Ltd.
- 454 Melià, P., Schiavina, M., Rossetto, M., Gatto, M., Frascchetti, S. & Casagrandi, R. (2016)
455 Looking for hotspots of marine metacommunity connectivity: a methodological
456 framework. *Scientific Reports*, **6**, 23705.

- 457 Neubauer, P., Jensen, O.P., Hutchings, J.A. & Baum, J.K. (2013) Resilience and recovery of
458 overexploited marine populations. *Science*, **340**, 347–349.
- 459 Ortuño Crespo, G. & Dunn, D.C. (2017) A review of the impacts of fisheries on open-ocean
460 ecosystems. *ICES Journal of Marine Science*, **74**, 2283–2297.
- 461 Pascual, M., Rossetto, M., Ojea, E., Milchakova, N., Giakoumi, S., Kark, S., Korolesova, D.
462 & Melià, P. (2016) Socioeconomic impacts of marine protected areas in the Mediterranean
463 and Black Seas. *Ocean & Coastal Management*, **133**, 1–10.
- 464 Populus, J., Vasquez, M., Albrecht, J., Manca, E., Agnesi, S., Al Hamdani, Z., Andersen, J.,
465 Annunziatellis, A., Bekkby, T., Bruschi, A., Doncheva, V., Drakopoulou, V., Duncan, G.,
466 Inghilesi, R., Kyriakidou, C., Lalli, F., Lillis, H., Mo, G., Muresan, M., Salomidi, M.,
467 Sakellariou, D., Simboura, M., Teaca, A., Tezcan, D., Todorova, V. & Tunesi, L. (2017)
468 *EUSeaMap. A European Broad-Scale Seabed Habitat Map*. Ifremer.
- 469 Pujolar, J.M., Schiavina, M., Di Franco, A., Melià, P., Guidetti, P., Gatto, M., De Leo, G.A. &
470 Zane, L. (2013) Understanding the effectiveness of marine protected areas using genetic
471 connectivity patterns and Lagrangian simulations. *Diversity and Distributions*, **19**, 1531–
472 1542.
- 473 Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P. & White, A.T. (2004) Marine
474 reserves benefit local fisheries. *Ecological Applications*, **14**, 597–606.
- 475 Sala, E., Ballesteros, E., Dendrinou, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S.,
476 Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B.,
477 Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli,
478 F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F. &
479 Zabala, M. (2012) The Structure of Mediterranean Rocky Reef Ecosystems across
480 Environmental and Human Gradients, and Conservation Implications. *Plos One*, **7**,
481 e32742.
- 482 Treml, E.A., Ford, J.R., Black, K.P. & Swearer, S.E. (2015) Identifying the key biophysical
483 drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the
484 sea. *Movement Ecology*, **3**, 17.
- 485 Watson, J.R., Kendall, B.E., Siegel, D.A. & Mitarai, S. (2012) Changing seascapes, stochastic
486 connectivity, and marine metapopulation dynamics. *The American Naturalist*, **180**, 99–
487 112.
- 488 Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J.,
489 Fulton, E.A., Hutchings, J.A. & Jennings, S. (2009) Rebuilding global fisheries. *Science*,
490 **325**, 578–585.
- 491 Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B. & Gonçalves, E.
492 (2018) Marine partially protected areas: drivers of ecological effectiveness. *Frontiers in*
493 *Ecology and the Environment*, **16**, 381–387.

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 .

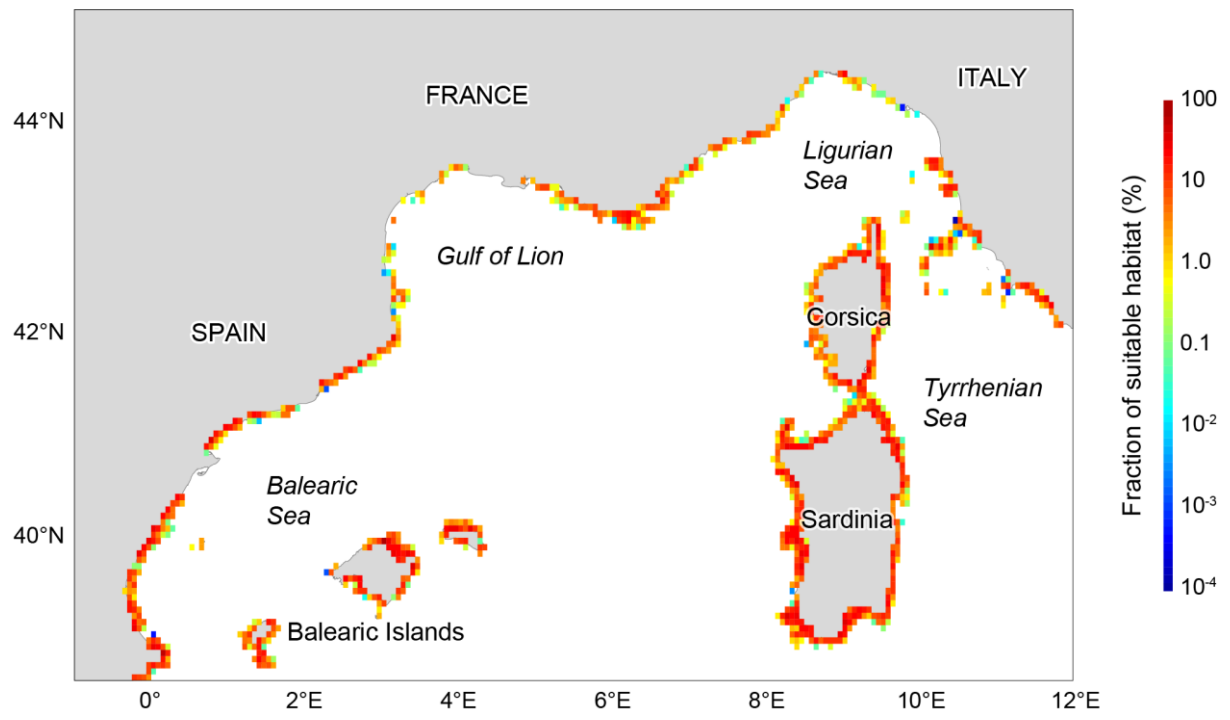
512

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.

523

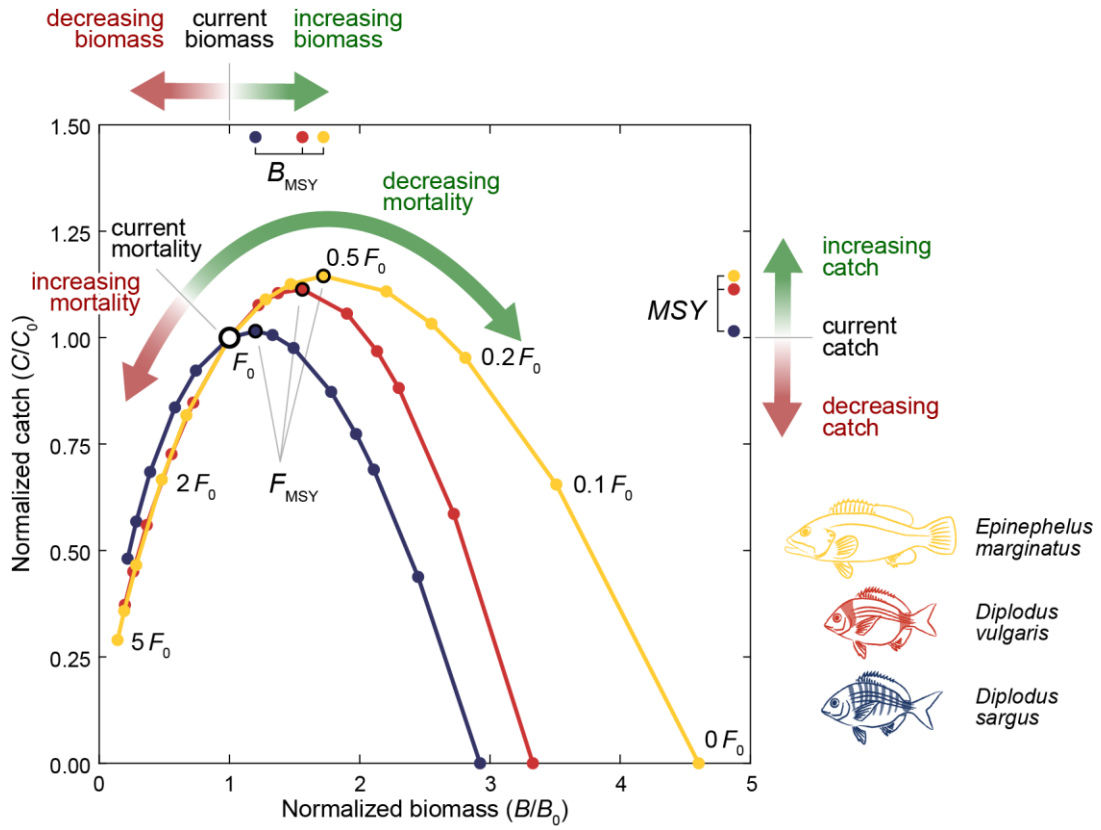


524

525

526

Fig. 1

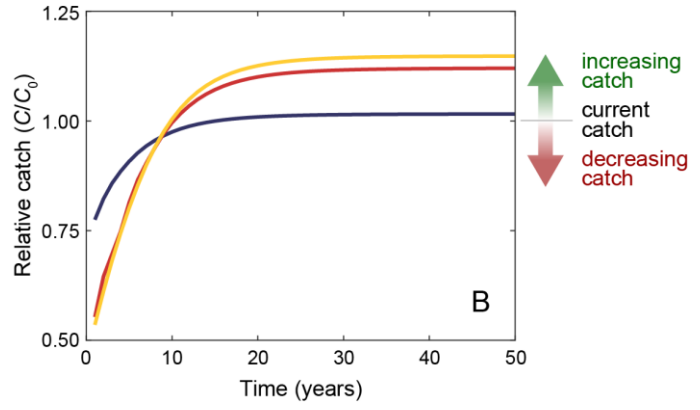
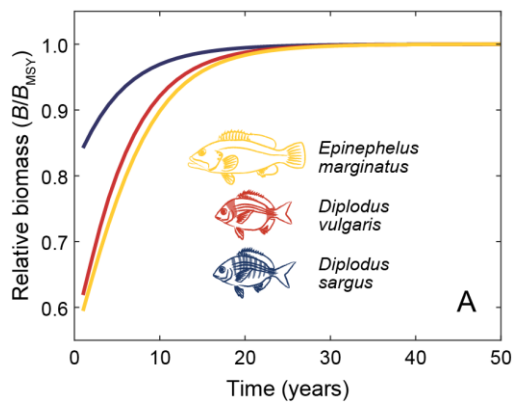


527

528

529

Fig. 2



530

531

532

Fig. 3

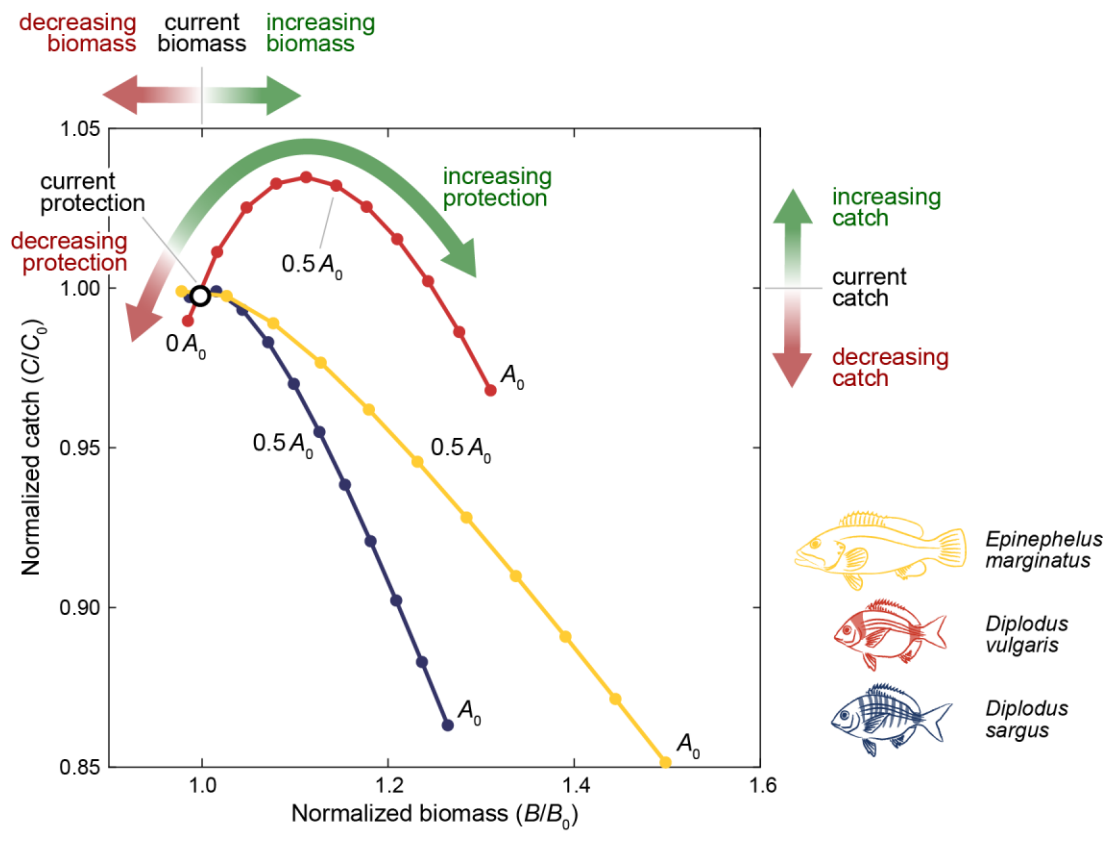
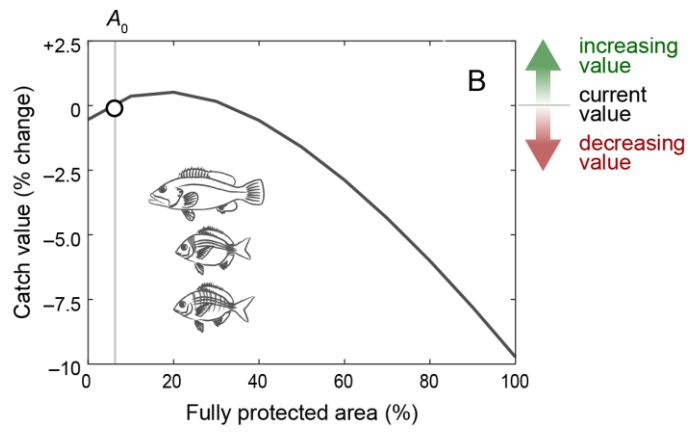
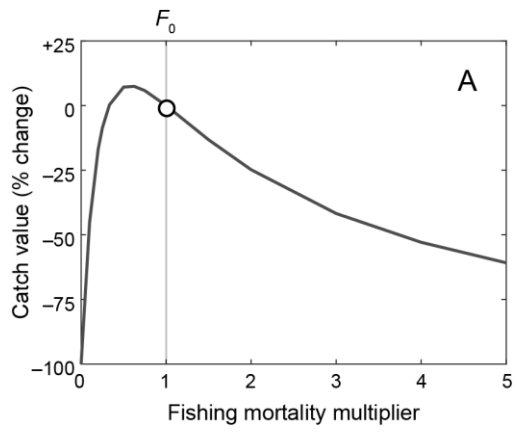


Fig. 4

533

534

535



536

537

Fig. 5