

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

4

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

- 8
- ⁹ ¹Dipartimento di Elettronica, Informazione e Bioingegneria, Politecnico di Milano, Via Ponzio 34/5, 20133
- 10 Milano, Italy.
- ²Université Côte d'Azur, CNRS, UMR 7035 ECOSEAS, Parc Valrose 28, Avenue Valrose, 06108 Nice, France.
- ³Stazione Zoologica "Anton Dohrn" sede interdipartimentale di Palermo, Italy
- ⁴CoNISMa, Piazzale Flaminio 9, 00196 Roma, Italy.
- ⁵Dipartimento di Scienze della Terra e del Mare (DiSTeM), Università di Palermo, Via Archirafi 20, 90123
- 15 Palermo, Italy
- ⁶National Center for Scientific Research, PSL Université Paris, CRIOBE, USR3278 CNRS-EPHE-UPVD,
- 17 Maison des Océans, 195 rue Saint-Jacques 75005 Paris, France.
- 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
- legends: 301); tables: 0; figures: 5; references: 61

29 Abstract

- Most fish stocks worldwide are overfished, and many fisheries management strategies
 have failed to achieve sustainable fishing. Identifying effective fisheries management
 strategies has now become urgent.
- Here, we developed a spatially-explicit metapopulation model accounting for seascape
 connectivity in the Mediterranean Sea, and parameterized it for three ecologically and
 economically important coastal fish species: *Diplodus sargus*, *Diplodus vulgaris* and
 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.
- 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

- 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**

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

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

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

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

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

105 **2 Methods**

106 **2.1 Case study**

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

118

2.2 Metapopulation model

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

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

141 2.2.2 Connectivity assessment

To evaluate seascape connectivity among local populations (i.e. among model cells), we 142 carried out Lagrangian simulations of larval dispersal across the study area with an 143 individual-based biophysical model. The physical component of the model was based on daily 144 average current velocity fields made available through the Copernicus Marine Environment 145 Monitoring Service (marine.copernicus.eu). Velocity fields, produced by the Mediterranean 146 Sea physics reanalysis (Fratianni et al. 2014), had a 1/16° (~6–7 km) horizontal resolution and 147 covered 72 unevenly spaced vertical levels. Lagrangian particles were released according to 148 the reproductive schedule of each species and tracked for the duration of the whole larval 149 phase. Simulations covered a 12-year-long time horizon (2004-2015). Results were 150 aggregated across a grid with the same resolution of the ocean circulation dataset $(1/16^{\circ})$ and 151 used to derive a set of connectivity matrices for each species and each year. The element 152 $c_{\{i,j,t\}} = \frac{n_{i \to j,t}}{n_{i,t}}$ of the connectivity matrix C(t) is the ratio between $n_{i \to j,t}$ (i.e. the number of 153

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

158 **2.2.3 Protection**

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

172 **2.2.4 Population dynamics**

Metapopulation dynamics were described by subdividing the stocks of the three species into subpopulations according to the same horizontal grid used for the connectivity assessment. To account for the heterogeneous distribution of suitable habitat within the study area, each cell was further subdivided into 30×30 sub-cells matching the spatial resolution of the bathymetric grid. The marine surface area A_i of each cell *i* was evaluated as the sum of the areal extent of its sub-cells with a valid bathymetric value. For each cell *i*, we calculated the surface area of suitable habitat A_i^{SH} as the area of the geometric intersection between the portion of cell between 0–50 m depth and the polygon of the suitable substrate. Only the cells with non-zero A_i^{SH} score (949 cells in total) were included in the metapopulation model (Fig. 1). Each subpopulation was subdivided into age classes (15 for *D. sargus*, 9 for *D. vulgaris* and 20 for *E. marginatus*), whose dynamics were described by taking into account both the local demographics and the exchange of larvae under the action of the currents.

185 2.3 Fisheries management scenarios

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

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

To evaluate the economic implications of the different scenarios tested, we estimated also the total value of catch (TVC) obtained from the fishery of the three study species. TVC was 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 species *k* averaged over the last 10 years of simulation. The relative change of TVC for each scenario was expressed as a percent change with respect to the TVC of the baseline simulation. Market prices were considered, based on an informal ex-vessel survey carried out across the study area, to be 20 EUR/kg for *D. sargus*, 18 EUR/kg for *D. vulgaris*, and 25 EUR/kg for *E. marginatus*.

209 **3 Results**

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

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

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

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

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

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

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

3.3 Economic consequences of the analysed scenarios

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

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

265 **4 Discussion**

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

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

Achieving MSY requires that fishing mortality rates be significantly reduced (by one quarter for *D. sargus* and one half for *D. vulgaris* and *E. marginatus*). In practice, this could be achieved through a range of management tools including both input (e.g. gear restrictions,
reduction of fishing capacity) and output controls (e.g. reduction in allowable catch).
Additionally, we show that in the medium/long term (10–20 years), such a prospect of fishery
recovery would simultaneously generate increases in stock biomass (17–42% depending upon
species), fisheries catch (2–13%) and, consequently, revenues for the fishery sector (8% of
increase in the total value of catch).

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

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

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

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

327 Authors' contributions

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

332

333 Acknowledgements

The present work has been carried out in the framework of the SafeNet project, funded by the 334 European Commission, Directorate General for Maritime Affairs and Fisheries (grant 335 SI2.721708 "Marine protected areas: network(s) for enhancement of sustainable fisheries in 336 EU Mediterranean waters" (MARE/2014/41)). Additional funding came from the European 337 Union's Horizon 2020 research and innovation programme (grant 641762 338 "ECOPOTENTIAL: Improving future ecosystem benefits through Earth observations"). 339 340

341 **References**

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

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

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

- Neubauer, P., Jensen, O.P., Hutchings, J.A. & Baum, J.K. (2013) Resilience and recovery of
 overexploited marine populations. *Science*, 340, 347–349.
- Ortuño Crespo, G. & Dunn, D.C. (2017) A review of the impacts of fisheries on open-ocean
 ecosystems. *ICES Journal of Marine Science*, 74, 2283–2297.
- Pascual, M., Rossetto, M., Ojea, E., Milchakova, N., Giakoumi, S., Kark, S., Korolesova, D.
 & Melià, P. (2016) Socioeconomic impacts of marine protected areas in the Mediterranean
 and Black Seas. *Ocean & Coastal Management*, 133, 1–10.
- Populus, J., Vasquez, M., Albrecht, J., Manca, E., Agnesi, S., Al Hamdani, Z., Andersen, J.,
 Annunziatellis, A., Bekkby, T., Bruschi, A., Doncheva, V., Drakopoulou, V., Duncan, G.,
 Inghilesi, R., Kyriakidou, C., Lalli, F., Lillis, H., Mo, G., Muresan, M., Salomidi, M.,
 Sakellariou, D., Simboura, M., Teaca, A., Tezcan, D., Todorova, V. & Tunesi, L. (2017) *EUSeaMap. A European Broad-Scale Seabed Habitat Map.* Ifremer.
- Pujolar, J.M., Schiavina, M., Di Franco, A., Melià, P., Guidetti, P., Gatto, M., De Leo, G.A. &
 Zane, L. (2013) Understanding the effectiveness of marine protected areas using genetic
 connectivity patterns and Lagrangian simulations. *Diversity and Distributions*, **19**, 1531–
 1542.
- Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P. & White, A.T. (2004) Marine
 reserves benefit local fisheries. *Ecological Applications*, 14, 597–606.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S.,
Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B.,
Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli,
F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F. &
Zabala, M. (2012) The Structure of Mediterranean Rocky Reef Ecosystems across
Environmental and Human Gradients, and Conservation Implications. *Plos One*, 7,
e32742.

- Treml, E.A., Ford, J.R., Black, K.P. & Swearer, S.E. (2015) Identifying the key biophysical
 drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the
 sea. *Movement Ecology*, 3, 17.
- Watson, J.R., Kendall, B.E., Siegel, D.A. & Mitarai, S. (2012) Changing seascapes, stochastic
 connectivity, and marine metapopulation dynamics. *The American Naturalist*, **180**, 99–
 112.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J.,
 Fulton, E.A., Hutchings, J.A. & Jennings, S. (2009) Rebuilding global fisheries. *Science*,
 325, 578–585.
- Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B. & Gonçalves, E.
 (2018) Marine partially protected areas: drivers of ecological effectiveness. *Frontiers in Ecology and the Environment*, 16, 381–387.

494 **Figure legends**

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

497

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

507

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

512

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

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





Fig. 2



531

Fig. 3





Fig. 4



537

Fig. 5